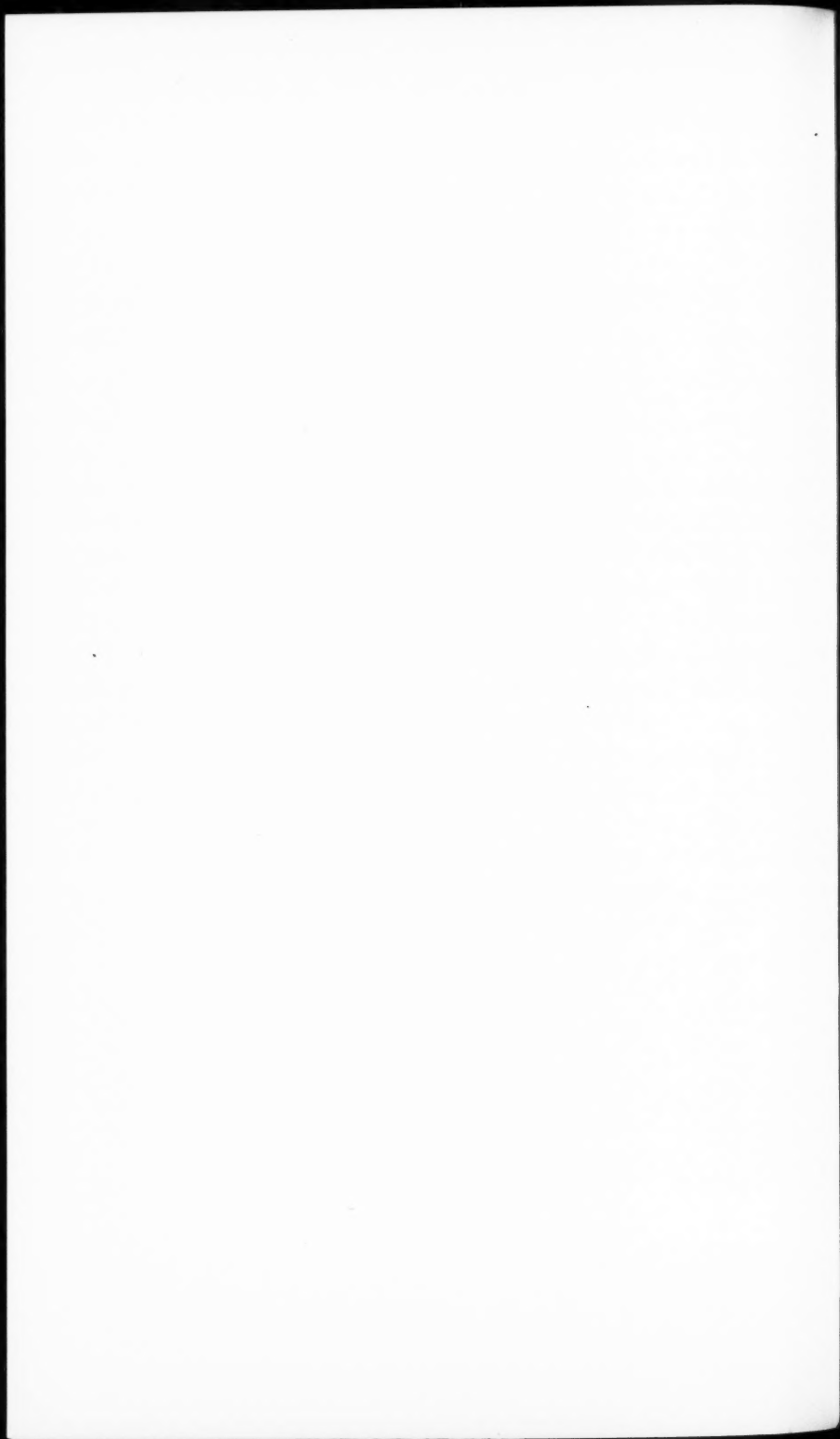


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ECOLOGICAL RELATIONS OF PONERINE AND OTHER
ANTS TO TERMITES

BY WILLIAM MORTON WHEELER



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PART I. ANTS OF THE GENUS TERMITOPONE GEN. NOV.

SPECIMENS of an unusually interesting, shining, jet-black Ponerine ant, which has long been cited in our lists as *Euponera* (*Mesoponera*) *laevigata* (F. Smith), were received recently from Dr. Alfred E. Emerson with the remark that he had observed them during the summer of 1935 in the act of raiding termite-colonies on Barro Colorado Island in the Canal Zone. This ant is closely related, both structurally and ethologically, to two other species from South America, *E. (M.) marginata* (Roger) and *Neoponera commutata* (Roger). The three, as I shall endeavor to show, constitute an economically important though neglected group of Ponerines, a distinct genus, in fact, for which I propose the name TERMITOPONE, with *laevigata* as the genotype. I am greatly indebted to Dr. Emerson not only for stimulating my interest in these insects but also for generous permission to quote from his unpublished field-notes and for revising the termite names in the following pages. I am indebted also to Dr. C. P. Haskins for contributing observations on *laevigata* and a specimen of its hitherto unknown male. Before the highly specialized behavior of each of the three species can be considered, it will be advisable to justify my radical change in their generic status and to redescribe their castes. In the second half of the paper I have been led, or perhaps misled, into attempting a general account and classification of the known relations between ants and termites, a subject which has become increasingly intricate with the rapid accumulation of observations and the various attempts at their interpretation.

Termitopone laevigata (F. Smith) (Fig. 1)

T. laevigata and *T. marginata* are closely related and were originally placed by their authors in the old genus *Ponera* of Latreille, but later transferred by Emery and Dalla Torre to *Pachycondyla*. In 1901 Emery shifted them with a number of other Neotropical and Palearctic species to his genus *Euponera*, which was so heterogeneous that he divided it into four subgenera: *Mesoponera*, *Euponera sens. str.*, *Brachypone* and *Trachymesopus*. At the present time all of these should, perhaps, be raised to generic rank. That Emery was quite aware of the diversity of the species which he had placed in

Mesoponera is apparent from his remark in the "Genera Insectorum" (1911): "This subgenus is extremely heterogenous and represents a classificatory residue; it should, no doubt, be subdivided later." Certainly he could not fail to notice that *laevigata* and *marginata* are conspicuously different in habitus from all the other species of Mesoponera. Removing them from the subgenus and genus in which he placed them leaves the "classificatory residue" more homogeneous, though in my opinion still too heterogeneous to escape future emendation.

Laevigata was originally described from a worker specimen taken by H. W. Bates at Ega, in Amazonas, Brazil, but Smith's description is so inadequate that in 1890 Emery redescribed specimens from Costa Rica under the name *Pachycondyla gagatina*. This synonym might have been avoided if Mayr in 1886 had more minutely redescribed the type which he examined in the British Museum. He notes only that it "is a species which I do not venture to place in any genus," and adds that "the clypeus is as in *Pachycondyla*, a carina is not present on the cheeks, the eyes are placed anteriorly, the petiole is cubical, somewhat narrowed anteriorly, similar to that of *Lobopelta chinensis*, the claws are simple." Since the characters mentioned by Mayr are as insufficient as those of Smith to distinguish *laevigata* from *marginata* I requested my friend Mr. Horace Donisthorpe to re-examine the type. He reports that "the proportions of the length to width of the head are as 11 to 7 (from tips of mandibles), the mandibles are uniformly convex, without a ridge, the antennal foveae and front longitudinally (obliquely) striate, the total length (from tip of mandible) 8.7 mm." These characters show that Smith's *laevigata* is indeed quite distinct from Roger's *marginata*, as had usually been assumed. In the sequel it will be shown that the geographical ranges of the two species are also distinct.

Only the worker of *laevigata* has been known heretofore, and the very interesting fact has been overlooked that this caste is dimorphic. Both the specimens collected by Dr. Emerson and fine series taken by Mr. Phil Rau in 1932 and more recently by Dr. Haskins in the same locality show that the differences between the major and minor workers are similar to those described by Arnold (1916) and myself (1922) in the only Ponerine ant previously known to have dimorphic workers, namely the African *Megaponera foetens* Fabr. (see p. 185). In fact, the genus Termitopone seems to be very closely related to Megaponera. Even the basal tooth of the tarsal claws, which Emery used as a diagnostic character to separate Megaponera from Ophthal-

mopone, Neoponera, Pachycondyla, Euponera and Pseudoponera, is present as a distinct vestige. Moreover, the preocular carinae of *M. foetens* are quite as pronounced as in *commutata*, which I am including in Termitopone as the type of a new subgenus, *Syntermitopone*. I append descriptions of all three castes of *laevigata*.

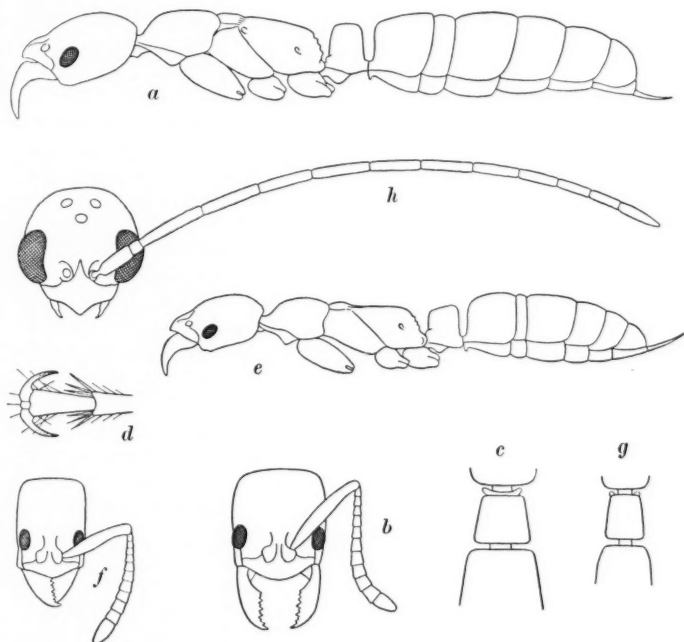


FIGURE 1. *Termitopone laevigata* (F. Smith). a, worker major, in profile; b, head of same, dorsal view; c, petiole, dorsal view; d, last tarsal joint, showing vestiges of teeth near bases of claws; e, worker minor, in profile; f, head of same; g, petiole, dorsal view; h, head of male, dorsal view.

Worker major. (Fig. 1 a-d.) Length 8.5-10 mm.

Slender; head without the mandibles one-fifth longer than broad, very nearly as broad in front as behind, with straight posterior border and feebly convex sides. Eyes feebly convex, somewhat longer than their distance from the anterior border of the head. Cheeks in front

of the eyes subcarinate. Mandibles with nearly straight external borders, their upper surfaces convex, without longitudinal groove, their apical border long, with 10 to 12 alternately large and small teeth. Antennal scapes reaching to the posterior border of head; funicular joints 1-6 longer than broad, 7-10 as broad as long. Pronotum distinctly marginate on the sides; base of epinotum fully twice as long as the sloping, laterally crenately marginate declivity and passing into it without a distinct angle. Petiole subcuboidal, from above trapezoidal, as long as broad, with straight anterior, lateral and posterior borders; node in profile higher than long, but slightly narrowed above, its anterior surface slightly concave, its dorsal surface straight and horizontal, its posterior surface feebly convex. Postpetiole as long as or slightly longer than broad.

Very smooth and shining, with coarse, scattered, piligerous punctures. Antennal foveae and front longitudinally striate, the striae diverging posteriorly on the latter; sides of epinotum and petiolar node longitudinally striate, the striae parallel, sharper and more regular than on the head, nearly horizontal on the epinotum, on the petiole sloping downward and backward.

Hairs yellowish, sparse, coarse, of uneven length, rather long on the body, decidedly shorter on the scapes and legs. Appressed pubescence absent except on the middle and hind coxae and on the venter, where it is sparse and longer.

Jet black; mandibles, frontal lobes, funiculi, metasternal angles of epinotum, sting, portions of terminal gastric segments, tarsi, tips of femora, extensor surfaces of tibiae and in some specimens also of femora, red; tibial spurs yellow.

Worker minor. (Figs 1 e-g.) Length 5-7 mm.

Differing from the major in its smaller size and longer head, which is fully one and one-fourth times as long as broad and has straight, parallel sides, feebly convex posterior border and more flattened eyes. Scapes of antennae proportionally shorter, funicular joints, except the first and last, broader than long. Petiole and postpetiole longer than broad. Striae absent on antennal foveae and front; on the sides of the epinotum less pronounced and occupying a smaller area on the sides of the petiole.

Pilosity and color as in the major, except that the mesosterna and sides of the petiole often have pronounced blue reflections and that the tips of the scapes and regions which are red in the major are more yellowish red or testaceous.

Female (undescribed). Length 11 mm.

Similar to the major worker. Striae on antennal foveae and front coarser and extending nearly to the posterior border of the head. Eyes larger and more convex; ocelli small. Lateral marginations of pronotum even more pronounced. Epinotum with convex base, which is only half as long as the straight, sloping declivity. Petiole more narrowed above in profile and more scale-like than in the worker major, the posterior surface strongly marginate laterally. Gaster broader and shorter. The striae form a small patch on each side of the pronotum but they are not developed on the mesepisterna and on the sides of the epinotum and petiole are much coarser than in the worker major. On these regions, and especially on the epinotum they might more properly be described as rugae.

Pilosity as in the worker major but the hairs on the postpetiole and gaster are more numerous and longer and the pubescence on the venter is more abundant. Sides of thorax and petiole with pronounced blue reflections. Wings distinctly and uniformly infuscated; veins brown, pterostigma dark brown.

Male (undescribed). (Fig. 1 *h*.) Length 8.5–9 mm.

Slender; head small, as long as broad, semi-circular behind, the eyes, which are rather large and convex, nearly half as long as the sides, cheeks very short. Mandibles small and vestigial, edentate, widely separated, their tips acute and slightly curved. Clypeus convex, its anterior border projecting and subangulate. Antennal scapes about twice as long as broad, thickened apically; funiculi slender, first joint nearly as broad as long, remaining joints gradually decreasing in length toward the tip, the second fully six times as long as broad and about one-fifth longer than the third. Thorax elongate, narrowed anteriorly and posteriorly; pronotum with straight, submarginate sides; promesonotal suture deeply impressed; mesonotum evenly convex, as long as broad, without notauli; scutellum very convex; epinotum angulate in profile, its base feebly convex and about half as long as the declivity, which is sharply marginate on the sides and above. Petiole from above somewhat longer than broad, the node sharply trapezoidal, laterally almost concave, with acute, subdentate posterior corners, in profile as high as long, cuneate, with flattened anterior and posterior surfaces, rounded dorsal surface and posteriorly marginate, coarsely crenate lateral borders. Gaster long and slender; postpetiole as broad as long, not sharply truncated anteriorly. Pygidium terminating in a strong, deflected spine; genitalia small, retracted; subgenital plate rather narrow, rounded and entire. Legs short and slender. Wings very short (6. mm.).

Shining; head and thorax somewhat less so than the abdomen, sparsely and feebly punctate; mesonotum finely, longitudinally striate, scutellum coarsely punctate posteriorly and rugose laterally; epinotum, including its declivity, longitudinally rugose; gaster and petiolar node very smooth and shining.

Hairs yellowish, short, rather coarse, uneven and sparse, longest on the head and posterior border of the petiole, shortest on the legs, conspicuously dense on the sides of the subgenital plate. Pubescence subappressed, generally distributed, but less abundant on the dorsum and not long enough to obscure the shining surface.

Jet black; head and pronotum with blue reflections; mandibles, mouthparts and ventral scutes of the two last gastric segments brownish yellow, tibiae obscurely reddish, especially on their extensor surfaces. Wings infuscated, with dark brown veins and pterostigma.

I have seen specimens of *laevigata* from all but the first and last of the following localities:

Brazil: Ega, Amazonas (H. W. Bates), type-locality ♂; Pará (C. F. Baker) ♀.

British Guiana: Kartabo (W. M. Wheeler) ♂; Kaieteur (F. E. Lutz) ♂.

Trinidad: Capara (P. B. Whelpley) ♂; Mt. St. Benedict (J. G. Myers) ♂.

Ecuador: Gualaquiza and vicinity (W. von Hagen) ♂.

Panama: Barro Colorado I. (C. P. Haskins ♂ ♀ ♂, P. Rau ♂, A. E. Emerson ♂).

Costa Rica: Jimenez (A. Alfaro) ♂.

The var. *whelpleyi*, which I described in 1922 from Trinidad, should be regarded as a synonym of *laevigata*, since the characters of the single specimen, a large minor worker or media, on which it is based, fall within the normal range of variability of the colony.

The following observations made by three different entomologists on Barro Colorado Island throw much light on the behavior of *laevigata*. Dr. C. P. Haskins, who has generously given me specimens of this ant, informs me that at about 3:00 p.m. on August 15, 1930 he encountered it in a compact column about four feet long and three or four inches wide crossing one of the numerous trails that have been hewn through the primitive forest on the island. Accompanying the mass of workers, which were in all probability migrating to a new nesting site, were several males and winged females.

A few years later Mr. Phil Rau found nests of *laevigata* which he

described (1933) as being in the ground under a log or heavy leaf and as sometimes extending up into the log.¹

Probably the termite raids of these ants do not begin till the rainy season sets in. At least I saw no traces of them during my latest visit to the island, towards the end of the dry season (April 3-12, 1935). Dr. Emerson was more fortunate later in the same year, when he succeeded in witnessing the raids on three occasions, as will be seen from the following excerpts from his notes.

On July 14 he came upon a column of about 500 workers "returning from a raid on termites and marching for the most part in single file. About one out of every three ants carried from one to five worker or soldier termites in its jaws. They were returning to their nest which they entered through a small hole in the leaf-débris of the forest floor." He was unable to locate the raided termite colony. "The column was about 20 feet long, with about 25 ants to the foot. The termites carried were soldiers and workers of *Amitermes beaumonti* Banks and workers of *Heterotermes tenuis* (Hagen), both characteristic species of the dead wood on the forest floor. The ants were carrying no other insects but termites."

September 9 Dr. Emerson encountered a column of more than a hundred *laevigata* workers with termites (*Anoplotermes* (*Speculitermes*) *sp.*) in their jaws while others were seen returning without any prey. He traced the column to a distance of 25 feet along the trail to a hole in the ground from which the termite-laden ants were emerging. They were evidently raiding an underground gallery, but subsequent digging failed to disclose the termites. Later he found a few paralyzed workers and soldiers of *Heterotermes tenuis* under a leaf near their trail but no termites of this species were seen in the ants' jaws.

A few days later (September 13) he encountered *laevigata* workers entering holes in a log and raiding a colony of *H. tenuis*. Sawdust was seen around the edges of the holes, which had probably been made by the ants, but they were not actually seen in the act of breaking into the termitary. Dr. Emerson writes me that this and the preceding observations were made towards noon.

While I am writing this paper Dr. Haskins informs me that he has just found (February 1936) a large *laevigata* colony nesting both in the soil and a small superjacent log on Barro Colorado Island. The

¹ I unfortunately misidentified Mr. Rau's specimens as *marginata*. His series comprised a number of minor workers, which lacked the striae on the head, a character which I erroneously supposed to be peculiar to Roger's species.

workers of the colony were aggressive and made active use of their stings while he was collecting some of the males and winged females.

Termitopone marginata (Roger). (Fig. 2)

Roger (1861) published an excellent description of all three castes of this ant, and Gallardo (1918) has more recently redescribed it, with figures of the worker and male. Neither of these authors, however, noticed that the worker is dimorphic, probably because they had only a few specimens and because the differences in size and in the length of the head and funicular joints are less marked between the major and minor than in the corresponding phases of *laevigata*. The differences between the various castes of the two species will be apparent from the following description of *marginata*:

Worker major. (Fig. 2 a-c.) Length 11-12 mm.

Decidedly larger and stouter than *laevigata*; head shorter and broader, without the mandibles less than one-sixth longer than broad, more narrowed anteriorly. Mandibles somewhat more strongly deflected distally, with more concave external borders, their apical borders with about a dozen blunter and less unequal teeth, their dorsal surface strongly convex or swollen along the external and abruptly depressed along the apical border, which produces the appearance of being grooved. The depressed area widens basally and bears large piligerous punctures which are more conspicuous than in *laevigata*. Antennal scapes reaching to the posterior border of the head; funicular joints 1-6 longer than broad, 7-10 as broad as long. Pronotum almost as sharply marginate on the sides as in *laevigata*; epinotum with the base and declivity subequal and meeting at a more distinct obtuse angle. Petiolar node with the dorsal surface in profile more convex above and more rounded at its junctions with the anterior and posterior surfaces. Gaster proportionally shorter and stouter than in *laevigata*.

Sculpture, pilosity and color as in that species, but there are no striations on the head and sides of petiolar node and the scapes and cheeks are red like the mandibles, tarsi and extensor halves of the femora and tibiae.

Worker minor. (Fig. 2 d, e.) Length 9-10 mm.

Differing from the worker major in the proportionally longer and more rectangular head, which is fully one and one-fifth times as long as broad without the mandibles, and in having the joints of the funiculi, except the first and last, distinctly broader than long. The appendages are darker, the antennal scapes and entire femora being black.

Female. (Fig. 2 h.) Length 13-14 mm.

Very similar to the major worker but the head even shorter, broader and more distinctly narrowed anteriorly. Eyes larger, twice as long as

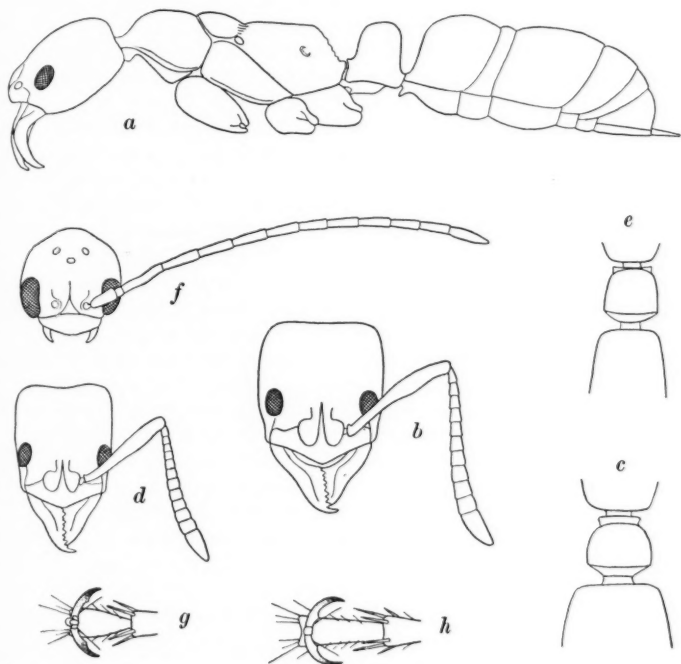


FIGURE 2. *Termitopone marginata* (Roger). *a*, worker major, in profile; *b*, head of same, dorsal view; *c*, petiole of same, dorsal view; *d*, head of worker minor; *e*, petiole of same; *f*, head of male; *g*, last tarsal joint of same, showing toothed claws; *h*, last tarsal joint of female, with vestigial teeth.

broad and placed obliquely; ocelli small. Epinotum and petiole much as in *laevigata*; postpetiole broader than long. Gaster more voluminous than in the worker major.

Sculpture, pilosity and color very similar, but sides of thorax with distinct bluish reflections. Wings as in *laevigata*, uniformly but not

strongly infuscated, with brown veins and dark brown pterostigma.

Male. (Fig. 2 f, g.) Length 11–13 mm.

Slender. Head small, narrower than the thorax, subcircular. Eyes proportionally smaller and distinctly less convex than in *laevigata*. Mandibles very small, triangular, acute but edentate, widely separated. Antennae rather short, filiform; scapes less than twice as long as broad; first funicular joint as long as broad; second joint about five times as long as broad, distinctly angulate near the middle, remaining joints gradually decreasing in length to the tip. Thorax resembling that of the female but more slender and with more prominent scutellum. Petiolar node narrowed above both anteroposteriorly and laterally, apically bluntly rounded. Gaster long and slender; pygidium terminating in a well-developed, flattened spine. Genitalia small and concealed, subgenital plate entire, with broadly rounded tip. Legs slender; tarsal claws distinctly toothed. Wings short (7 mm.).

Finely punctate, shining but appearing less so than the worker and female because of the grayish pubescence investing the body; erect hairs shorter than in the other castes. Black; thorax and abdomen with distinct blue reflections; mandibles, palpi, tips of antennal scapes, tarsi, streaks on the extensor surfaces of the femora and tibiae, genitalia and ventral scutes of the two last gastric segments, dull yellow. Wings slightly paler than those of the female, with paler brown veins.

T. marginata has been taken in the following localities:

Brazil: Rio Grande do Sul: São João del Rey, type-locality ♀ ♀ ♂; São Lourenço (*teste* Borgmeier), São Paulo (von Ihering, M. Savioz, A. Barbiellini) ♀ ♀ ♂, Upiranga, Franca, Ituverava (*teste* Borgmeier); Minas Geraes: Poços de Caldas (von Ihering), Pirapora; Paraná: Guayra; Matto Grosso: Corumba (J. C. Bradley) ♀; Goyaz: Chapada (Phila. Acad. Coll.) ♀.

Bolivia: Charubamba (N. Holmgren) ♀.

Paraguay: Paraná River (K. Fiebrig) ♀.

Argentina: Posadas, Misiones (C. Bruch, C. Lizer) ♀ ♀ ♂.

This list of localities shows that *marginata* has a decidedly more southern distribution than *laevigata*. It remains for future investigators to determine whether the ranges of the two species actually overlap in northern Brazil.

Nothing has been published on the habits of *marginata* but they are in all probability very similar to those of *laevigata*. That it feeds on termites is proved by the cabinet specimen collected by Dr. Bradley at Corumba, Matto Grosso, which still holds a worker termite in its jaws.

Termitopone (Syntermitopone subgen. nov.)
commutata (Roger) (Fig. 3)

This large and conspicuous jet-black ant was described by Latreille as long ago as 1802 as *Formica tarsata* but unfortunately confused with an Ethiopian species, *F. tarsata* Fabricius (now *Paltothyreus tarsatus*). Roger (1861) therefore changed the specific name to *commutata* and regarded the insect as a *Ponera*. Later it was shifted by Emery (1893) to *Pachycondyla* and finally, in 1901, to his genus *Neoponera*, mainly because of its possession of sharp preocular carinae. On turning to the "Genera Insectorum" (1911) we find that he divided the species of this genus into four groups, the first of which has *commutata* as its sole member. Thus he emphasized the marked difference between this ant and the other species of the genus. When we compare *commutata* with *laevigata* and *marginata* we are struck by the resemblances in general habitus. *Commutata*, however, differs from the two other species in its much greater size, the strict monomorphism of its workers, its sharp preocular carinae, proportionally larger and more medially placed eyes, proportionally shorter gaster and much feebler constriction between it and the postpetiole. Since these characters, in my opinion, have less than generic importance I regard *commutata* as the type of a new subgenus, for which I propose the name *Syntermitopone*. Its removal from *Neoponera* leaves that genus more homogeneous, while its general habitus and behavior as described below, favor its inclusion in *Termitopone*.

It is surprising that the male of *commutata* has never been seen by myrmecologists though the worker and female are not uncommon in collections and not infrequently cited in the literature. Equally surprising is the fact that no one during the past 134 years has seen fit to redescribe and figure this handsome insect. I may be pardoned, therefore, for inserting an account of its two known castes.

Worker. (Fig. 3.) Length 16-19 mm.

Head nearly square, without the mandibles slightly longer than broad, anteriorly as broad as or slightly broader than posteriorly, with straight subparallel sides and posterior border. Eyes large and convex, just in front of the middle of the head. Preocular carinae well-developed. Mandibles large, with concave external borders and uniformly convex dorsal surface, their apical borders bearing 17-19 blunt, alternately large and small teeth. Clypeus with broadly rounded, entire anterior border, posterior surface convex in middle, extending back between the frontal lobes which have thick, raised and laterally subangulate borders. Antennae long and stout; scapes

extending nearly one-third their length beyond the posterior borders of the head; all the funicular joints longer than broad, the first joint distinctly shorter than the second. Thorax long and narrow, decidedly narrower than the head; pronotum not marginate laterally, in profile sloping and somewhat flattened anteriorly, posteriorly straight and horizontal like the mesonotum and base of epinotum, promesonotal and mesoepinotal sutures strongly impressed, the latter longitudinally costate; base of epinotum about twice as long as the declivity which is sloping, concave in the middle and on each side strongly and crenately marginate. Petiole rather small, nodiform, from above trapezoidal and slightly narrowed anteriorly, about one and two-thirds times as long as broad; in profile higher behind than in front, the posterior surface perpendicular and slightly convex, crenately marginate laterally, the superior surface sloping anteriorly and forming a blunt, indistinct angle with the more abruptly sloping anterior surface. Postpetiole as long as broad, not sharply truncated anteriorly and not separated posteriorly by a pronounced constriction from the gaster, which is rather short, with its first segment broader than long. Sting long. Legs long and stout, middle and hind tibiae each with a large pectinated and smaller simple spur as in *laevigata* and *marginata*.

Very smooth and shining, with sparse piligerous punctures; mandibles subopaque, densely striolate-punctulate, with a series of coarse, piligerous punctures along their apical border. Clypeus and frontal lobes feebly striate; remainder of head, except occiput, sharply and regularly striate, the antennal foveae concentrically. On the front the striae diverge strongly towards the posterior corners where they turn ventrally and become continuous with straight, longitudinal striae on the cheeks and gula. Antennal scapes longitudinally striolate. Sides of epinotum and in part also the mesosterna longitudinally striate.

Erect hairs fulvous, sparse, coarse, of uneven length, moderately long on body, longest on clypeus and gula, much shorter on appendages, sub-appressed on tibiae. Pubescence greyish, fine, appressed, confined to antennal funiculi, middle and hind coxae.

Jet black; antennal insertions, metasternal angles of thorax, sting, terminal tarsal joints and posterior borders of postpetiole and gastric segments red or yellowish red; tibial spurs and dense pubescence on planter surface of fore basitarsi, yellow.

Female. Length 18-20 mm.

Very similar to the worker. Eyes larger; ocelli very small. Thorax nearly as wide as head; pronotum without the neck rectangular,

parallel-sided, about one-fifth broader than long; mesonotum transversely elliptical, nearly half again as broad as long; epinotum short, sloping, its base convex, passing into the somewhat shorter declivity without a distinct angle. Petiolar node in profile more narrowed above than in the worker, its dorsal surface shorter and forming a less distinct angle with the anterior surface. Abdomen larger; postpetiole broader than long. Wings short (13 mm.).

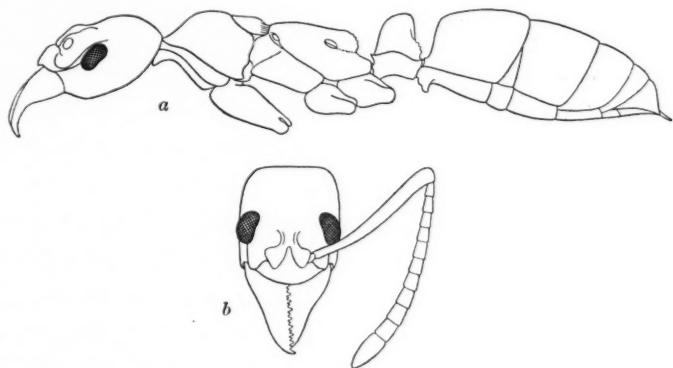


FIGURE 3. *Termitopone* (*Syntermitopone*) *commutata* (Roger). *a*, worker, in profile; *b*, head of same, dorsal aspect.

Sculpture, pilosity and color as in the worker, striae of head and epinotum somewhat coarser. Wings uniformly infuscated, with dark brown veins and pterostigma.

The geographical range of *commutata* embraces the lower, forested regions of the whole of South America north of the tropic of Capricorn. That it does not enter Central America is indicated by its omission from the "Biologia Centrali-Americana" and my failure to find it on various visits to Panama, Costa Rica and Guatemala. Forel seems not to have found it in the Santa Marta district of northern Colombia and it is not represented in collections made for me in that region by Dr. George Salt and Dr. P. J. Darlington. I have seen specimens from nearly all of the following localities:

Colombia: Rio Uapes ♀.

Peru: Chaquemayo (N. Holmgren) ♂; El Encanto and La Chorrera to La Sombra, Putumayo Distr. ♂ ♀; San Nicolas, Campamiento de

Pichis ♀; El Campamiento to Hacienda de Magdalena ♀ ♀, Hacienda de San Juan, Colonia de Perene ♀; Union de la Isla, Iquitos ♀; Rio Tioara, Parana ♀ (J. C. Bradley); El Campamiento, Colonia de Perene (W. T. M. Forbes) ♀.

Ecuador: Vicinity of Quito (Miss E. Naumann) ♀; Rio Boni Boisa (W. von Hagen) ♀.

Venezuela: Lower Orinoco (N. Weber) ♀.

British Guiana: Blairmont (F. X. Williams) ♀; Kartabo and vicinity (W. M. Wheeler, A. E. Emerson) ♀ ♀; Bartica and Aremu R. (W. Beebe) ♀; Wenamu R. (W. J. Lavarre) ♀; Kaieteur, Tukheit, Tumatumari and Potaro Landing (F. E. Lutz) ♀ ♀; Kamakusa and Mouth of Wenamu R. (H. O. Lang) ♀; Source of Essequibo R. (J. Ogilvie) ♀.

Dutch Guiana: Ongeljik, Bara R. and Zanderij Island (J. C. Bradley) ♀ ♀.

French Guiana: Cayenne (Jelski) ♀ ♀.

Brazil: Amazonas: Cururuzinho, Rio Autaz (A. Roman) ♀ ♀; Visto Alegre, Rio Branco (P. Bunting, J. Bequaert) ♀; Fonteboa, Manaos, Jabaty and Belem, Pará ♀; Rio Tocantins (Fruhstorfer) ♀; Obidos, Arima on the Rio Purus and Uassa Island (S. M. Klages) ♀ ♀; Puerto Velho (W. M. Mann) ♀ ♀; Matto Grosso: Cuyabá (F. Silvestri, W. M. Mann) ♀, Madeira-Mamoré R. R. (W. M. Mann) ♀; Goyaz: Chapada (Phila. Acad. Coll.) ♀.

Bolivia: San Firmin (N. Holmgren) ♀.

T. commutata is the most spectacular of our American termite-raiders both on account of its large size and striking appearance and because it preys exclusively on the species of a single genus, *Syntermes*, which comprises the largest representatives of the order Isoptera in South America. As we should expect, therefore, the geographical range of the ant is coextensive with that of its prey. I record in detail the observations that substantiate these statements, partly because of their intrinsic interest and partly because they furnish such an instructive illustration of the method whereby the repeated, fragmentary observations of the field naturalist can be made to yield behavioristic information which could not be obtained in the laboratory.

The earliest observation on the prey of *commutata* seems to have been made by Dr. F. E. Lutz, of the American Museum of Natural History. A specimen which he sent me from Kaieteur, British Guiana, with a *Syntermes* worker, bears the label "this ants' prey," and was recorded in my paper of 1916. In 1923 I referred to some

workers and females of *commutata* taken with termites during the fall of 1914 by Dr. A. Roman on the Rio Autaz, in Amazonas and labelled: "caught marching in single file and carrying large, thick-headed, yellowish brown termites." The latter were subsequently identified by Dr. Emerson as *Syntermes territus* Emerson. During the summer of 1920 he gave me a worker *commutata* which had been taken on June 11 of the same year by Dr. W. F. M. Forbes at El Campamiento, Col. Perene, Peru bearing a worker *Syntermes chaque-mayensis* Holmgren in its jaws.

Much more extensive observations on *commutata* were made by Dr. Emerson during the summer of 1920 and the spring of 1924 at and near Kartabo, British Guiana. His unpublished notes contain references to no less than 18 occasions on which he, and two on which Mr. J. F. M. Floyd, encountered *commutata* workers either transporting *Syntermes* or raiding their colonies. The termites, comprising both soldiers and workers, belonged to three different species, *S. snyderi* Emerson, *S. territus* Emerson and an undescribed form. Some of the more interesting notes are here reproduced.

"Kartabo, B. G. Sept. 9, 1920. *Syntermes* sp. preyed upon by *commutata*. Three of these ants were moving along close together, two of them each with two termite workers, the third with one."

"Kartabo, B. G. Oct. 14, 1920. I saw a column of 19 *commutata* travelling along in single file through the forest and followed it for 110 ft., when I gave up on account of the darkness. They travelled this distance in 17 minutes and seemed to be out to raid a termite nest. The other day I saw a similar file of what seemed to be the same species of ant also at dusk."

"Kartabo, B. G. Oct. 10, 1920. Between 5:30 and 6:00 p.m. I observed a large number of *commutata* (more than 100) raid a trail of *Syntermes territus*. The termites, of which soldiers and two kinds of workers were plentiful, formed an open trail on top of the ground. The ants, moving either in groups or singly, came down a small hill from their nest in the ground under some low bushy vegetation about 150 ft. from the termites and stridulated violently while moving back and forth from their nest. They attacked both the soldier and worker termites by stinging them and then carried them off to the nest. Occasionally termites were dropped after being stung and these were seen to be completely paralyzed. Many of the ants were seen with two termites in their mandibles, but most of them carried only a single one. The termites had evidently been cut off from their nest, which was not seen. These termites nest below the surface of the

ground in excavated galleries. Their trail ended abruptly where the ants were attacking and at the other end they milled about in a loop. They started off in a new direction soon after they were discovered but seemed to be lost and at the mercy of the ants, which kept returning after depositing their prey in the nest. In general the ants followed the same trail back to the nest without deviating very far to either one side or the other, although occasionally one would walk off the trail without getting lost. Dusk prevented my seeing the capture of the last termite. It was estimated that several hundred *Syntermes* were carried back to the Ponerine nest."

"Kartabo, B. G. March 8, 1924. A *commutata* worker was seen about dusk on the Paruni Trail with a soldier of *Syntermes territus* in its jaws. Further on I encountered about 100 of the ants returning from a raid, each carrying one or two termites. A little later, just as it was becoming too dark to see, I saw 18 empty-jawed individuals hurrying along in a file, but the darkness prevented me from following them very far."

"Kartabo, B. G. May 15, 1924. Saw a *commutata* worker carrying a worker *Syntermes snyderi*. A small fly (Acalyptate Muscid) followed along directly behind the ant as it walked with its prey. While I watched them for about two minutes the fly was never more than half an inch away from the ant."

Dr. J. Bequaert (1926) also observed *commutata* raiding *Syntermes* near Vista Alegre, on the Amazon. In this instance the prey belonged to two species, *S. grandis* (Rambur) and *S. brasiliensis* Holmgren. "These two large species of *Syntermes*," he says, "were observed in the savanna or campos of Vista Alegre, foraging in broad daylight, between 9 and 10 a.m., the weather being quite sunny. The soldiers and workers had spread over the soil but not in very large numbers and were busily engaged in collecting stalks and leaves of grasses and other low plants. The two species, of which *S. grandis* is much the larger, were working but a short distance apart, although on quite different areas. In each case the termites carried their burdens into a number of large openings leading into deep vertical channels in the sandy soil. The nest itself could not be reached. I also observed a column of the large ponerine ant, *Neoponera commutata* Roger, preying upon these termites, apparently attacking the workers only, of which they carried off many individuals. Soon after the ants appeared on the scene, the termites withdrew completely underground."

Bequaert's account differs from Emerson's in three particulars. The former found *commutata* in the open savanna country, whereas

this ant in British Guiana, as I repeatedly observed, belongs to the biocoenose of the shady forest floor, which is also frequented by several other large black Ponerines such as *Paraponera clavata* Fabr., *Pachycondyla crassinoda* Latr., *Neoponerina obscuricornis* Emery, *N. apicalis* Latr., *Ectatomma quadridens* Fabr. and a black, large-eyed Formicine, *Gigantiops destructor* Fabr. Furthermore, the raid observed by Bequaert occurred during the sunny morning hours though, according to Emerson, the expeditions and raids in British Guiana are crepuscular or nocturnal. He also found *commutata* carrying off both soldiers and workers of the termite while Bequaert says that the ants "apparently attacked the workers only." Perhaps these discrepancies may be explained by differences induced in the behavioristic responses of the ants by diversities in the habits of the Syntermes, which happen to belong to different species in the two localities.

The fact that *T. commutata* confines its raids to the huge species of the one genus Syntermes while *laevigata* and in all probability also *marginata* prey on small termites of various genera is of interest because it appears to reveal a definite correlation in size between the predator and its prey. Since the Ponerines feed their larvae directly with the prey and not, like the higher ants, with regurgitated juices from their crops, it is easy to understand why such large species as *commutata* should confine their attentions to the largest termites in their environment.¹ In this behavior there seems to be more than a vague analogy to the behavior of the solitary wasps which are known to adapt the volume of their prey to the alimentary requirements of their larvae.

That the male of *T. commutata* is quite unknown has been mentioned. Winged females are rare in collections, but dealated specimens are rather numerous among the material I have examined. Some of these were undoubtedly taken with workers and it would be interesting to know whether they participate in the raids. Solitary workers which I have occasionally seen wandering about the forests at Kartabo are probably scouts that locate the Syntermes colonies so that they can be more expeditiously attacked by the concerted columns. The solution of this and many other problems awaits the future investigator who has the opportunity and leisure to study this fascinating ant.

¹ The great size of these termites will be apparent from the measurements of the soldier in three of the species. This caste of *S. termitus* attains a length of 16-17 mm. of *S. dirus* 19 mm. and of *S. snyderi* 22 mm. The only other termite in the New World with a soldier of comparable dimensions is the Californian *Zootermopsis angusticollis* (Hagen) which measures 15-19 mm.

There is one other aspect of the relation of *commutata* to *Syntermes* that may be of interest to the zoogeographer who is collecting data to support the contention that the land-masses of South America and Africa were once connected. *T. commutata* is in many respects so similar to the Ethiopian *Paltothyrcus tarsatus* (also a termite raider, *vide infra* p. 186) that, as we have seen, so competent an entomologist as Latreille confused the two species. Now it is interesting to note that *Syntermes*, the very special prey of *commutata*, is, according to Holmgren (1912), one of the most primitive among the group of genera which culminate in the African genus *Macrotermes*. Holmgren, therefore, places *Syntermes* very near *Acanthotermes* (with seven species confined to Africa) as an early offshoot of the Termitid line of descent from the Rhinotermitidae. Hence it would seem that the *commutata* and *Syntermes* may have been associated ecologically as predator and prey ever since the Middle or Lower Cretaceous, when the land-connection between South America and Africa was dissolved. If this is true *commutata* has persisted as a very stable species while a number of local species of its prey have been developing over South America as far south as the tropic of Capricorn. The stability of the ant is attested by the fact that, so far as known, it exhibits neither subspecies nor varieties in any part of its range, whereas each of the thirteen known species of *Syntermes* has a more restricted distribution as shown in the following list compiled from the works of Holmgren (1912), Silvestri (1923) and Emerson (1925):

Syntermes bolivianus Holmgren. Southern Bolivia.

brasiliensis Holmgren. Amazonas, Brazil.

chaquimayensis Holmgren. Peru and Bolivia.

colombianus Snyder. Colombia.

dirus (Klug). Brazil and Guiana.

grandis (Rambur). Amazonas, French and British Guiana.

molestus (Burmeister). Matto Grosso, Brazil.

obtusum Holmgren. Paraguay.

parallelus Silvestri. British Guiana.

peruanus Holmgren. Peru and Bolivia.

silvestrii Holmgren. Matto Grosso, Brazil.

snyderi Emerson. British Guiana.

terrillus Emerson. British Guiana and Brazil.

In connection with the African relations of *Syntermes* it is also interesting to note that the types of the small lestobiotic ant, *Carcara winifredae* Wheeler (1922), were taken by Dr. Emerson deep in a subterranean termitary of *Syntermes dirus* in British Guiana, and

that the African and Indomalayan species of *Carebara*, a genus formerly supposed to be confined to the Old World, are all associated with species of the family Termitidae. Three of the four known American species, *carinata* Santschi, of French Guiana, *anopthalma* Emery of Brazil and *mayri* Forel of Paraguay, concerning which we possess no ecological data, were all taken within the geographical range of the *Syntermes* and are therefore, like *winifredae*, in all probability associated with termites of that genus. (See p. 199 and Appendix A).

PART II. THE ECOLOGICAL RELATIONS BETWEEN ANTS AND TERMITES

When we turn from the consideration of such sharply defined cases of termitophagy as those described in the preceding pages to the more general interrelations of ants and termites our data seem vague and difficult to classify. Both of these groups of insects in the tropics exhibit great diversity of habits and vital needs. The satisfaction of these needs is determined, of course, not only by the marked specific differences of the phylogenetically established structure and physiology of the species and individuals but also by the exigencies of their social behavior. Compared with the vital needs of non-social insects, those of the longer-lived ants and termites appear, therefore, to be much more powerful, insistent and sustained. Moreover the interrelations of the two groups are greatly influenced by their very different alimentary and protective behavior, since most ants are enterprising, predatory foragers in the open, while the termites are vegetarian, cryptobiotic creatures, compelled to adopt a more stable type of nest architecture and to develop and maintain a merely defensive soldier caste. The very success of these cryptobiotic adaptations, manifested in the feebler motility of the termites, the atrophy of the eyes, except in the royal castes, the thinning of their integument and great increase of adipose tissue in their abdomens, have only increased their defenselessness and served to stimulate the aggressive appetites of the ants. The latter, therefore, have found a much richer supply of food in the termite castes of all stages than in other ants, because these, as a rule, have nutritive value only as larvae or pupae. The termitaries, moreover, may be invaded by terrestrial ants and parts of the gallery system usurped as very suitable habitations. Hence, while the chief enemies of ants are other ants, the fiercest and most implacable enemies of termites are not other termites, but ants.

The economic importance of ants throughout the world is ambiguous, since they may be regarded as beneficial insofar as they destroy noxious insects, but injurious insofar as they cultivate aphids and coccids on our food and forest plants, establish themselves in our dwellings, etc. In the tropics their relations to termites are certainly of even greater economic significance, but again ambiguously, because they are very useful to man when they prey on termites that destroy houses, ships, books, textiles, etc., but may be regarded as injurious when they prey on termites that are important agents in converting the rapidly accumulating dead vegetable matter into mould or humus.

Since no experimental investigations of the relations of ants to termites have been undertaken, all our knowledge is confined to the casual and often very fragmentary observations of collectors in the field. Their observations, which have been accumulating since the beginning of the century, have been reviewed from time to time, mainly by Wasmann (1901-'02, 1915), Hegh (1922) and Bugnion (1922). Even in 1901 the data were sufficiently numerous and diverse to lead Wasmann to attempt their classification. The various categories which he and Forel had previously established for the relations between different species of ants, between ants and their myrmecophiles and between termites and their termitophiles were naturally applied *mutatis mutandis* to the relations between ants and termites. There is, indeed, in each of the four series an obvious and interesting sequence of hypothetical stages which parallels the well-known sequence in other organisms from predatism through parasitism, or rather parasitoidism, to neutral or even mutualistic symbiosis.

We may distinguish the following five groups of ants according to their behavior towards the termites:

(1) Termitharpactic ants, or frankly hostile raiders, three species of which have been considered in the preceding pages. The Dorylinae, some Cerapachyinae and the dulotic Formicinae and Myrmicinae exhibit very similar behavior towards other ants.

(2) Cleptobiotic, or footpad-ants which wrest the termite prey from the raiders. Here the significant relations are really between different species of ants.

(3) Lestobiotic, or thief-ants—minute species that prey on the termite brood or disabled termites. Analogous relations obtain also between different species of ants.

(4) Inquiline ants, which either prey occasionally on the termites or in many cases, perhaps, merely inhabit portions of termitaries as

indifferent neighbors. This category corresponds to what I have called "pleiobiosis" among ants.

(5) Termitoxenic, or guest-ants which may actually live among the termites on a friendly footing, like the members of the mixed colonies of ants.

Inasmuch as the fourth category is too vague and the fifth, so far as known, is represented only by a single case, the whole series differs from that of the ant to ant relationships in being far more heavily weighted at its predatory end. In other words, evolution from predatory towards symbiotic, or co-operative relations is far less advanced between ants and termites than between different species of ants. The raiders and footpads nest independently of the termites but the ants of the three remaining categories either preëempt galleries of termitaries after ousting or devouring the owners or excavate nests of their own in the partitions between and communicating by means of tenuous passages with the galleries or chambers of the termites.

Although the classification outlined above is fairly logical, many of the observations recorded in the literature can be assigned to the various categories only with considerable misgiving. This is due partly to the previously mentioned incompleteness of the observations and partly to the fact that some of the recorded cases seem to combine the peculiarities of more than one category. The fourth category, especially, is most unsatisfactory. As employed by previous writers, and as I am employing it in this paper, it is a mere catchall for observations that cannot at present be distributed with some show of certainty among the four other categories. Our classification, therefore, is crude and provisional and will doubtless be replaced eventually by another both more concise and more elaborate.

1. TERMITHARPAGY

The known termite-raiders among ants may be divided into two groups, the obligatory and the facultative. The former feed exclusively on termites and are all Ponerines, whereas the latter prey also on other insects and comprise Dorylines and Myrmicines as well as Ponerines. Since the obligatory forms exemplify only one of many kinds of highly specialized feeding, some other examples of this type of behavior may be reviewed before considering the species known to be exclusively termitophagous.

Specialized feeding is, of course, well-known in various tribes of Formicidae. Perhaps the most striking examples are furnished by the Attini among the Myrmicines, which feed exclusively on the

fungi which they cultivate on various vegetable substrata. In many ants the specialization may be temporary and due to seasonal abundance of particular foods, such as honey-dew, seeds or certain insects. In the more specialized ants the character of the food is often indicated, as in birds, by structural peculiarities of the mandibles. Although the Ponerinae are ancient and very primitive, they comprise, nevertheless, the following 37 genera or subgenera in which the mandibles are highly specialized and differ from those of most Formicids in having elongate, often more or less linear blades, with few or unusually modified teeth or other structural peculiarities: *Myrmecia*, *Mystrium*, *Stigmatomma*, *Amblyopone*, *Myopopone*, *Gnamptogenys*, *Emeryella*, *Thaumatomyrmex*, *Opisthoscyphus*, *Emeryopone*, *Centromyrmex*, *Typhloteras*, *Harpegnathos*, *Streblognathus*, *Dinoponera*, *Termitopone*, *Megaponera*, *Ophthalmopone*, *Eumecopone*, *Pseudoponera*, *Belonopelta*, *Simopelta*, *Dorylozelus*, *Trapeziopelta*, *Myopias*, *Plectroctena*, *Psalidomyrmex*, *Onychomyrmex*, *Leptogenys*, *Lobopelta*, *Odontopelta*, *Machaerogenys*, *Prionogenys*, *Anochetus*, *Stenomyrmex*, *Champsomyrmex* and *Odontomachus*. This list is the more impressive when we consider the rare occurrence of such mandibular modifications in the two much larger and more modern subfamilies, namely the Myrmicinae, in which the mandibles depart but slightly from the typical form, except in the genus *Strongylognathus* and the tribe Dacetoniini, and the Formicinae, in which only *Myrmoteras*, *Machaeromyrma* and *Polyergus* have aberrant mandibles like some of the genera in the foregoing list of Ponerinae. Unfortunately we have no data on the feeding habits of the great majority of these oddly mandibulate ants. It must be admitted also that these insects may use their mandibles not only in attacking particular kinds of prey but also for transporting the prey or brood, for excavating the nest or even for leaping, as in certain species of *Anochetus*, *Odontomachus*, *Harpegnathos* and *Acanthognathus*.

Perhaps food-specialization in the predatory Ponerinae had its phylogenetic origin in the well-known, very narrow preferences of their putative ancestors, the solitary Vespoids. At any rate, the Dorylinae and the higher subfamilies of ants, the Pseudomyrmicinae, Myrmicinae, Dolichoderinae and Formicinae, are, as a rule, either more general feeders or more plastic, since they can adapt themselves more readily than the Ponerinae to temporarily abundant food-supplies. All but one (*Platythyrea*) of the following Ponerinae belong to genera or subgenera with narrow or linear mandibles. In 1904 I called attention to the fact that the Texan *Leptogenys* (*Lobopelta*)

elongata feeds largely or exclusively on Oniscid Crustaceans (variously known as 'slaters,' 'woodlice' or 'sowbugs'), and Arnold (1915) has observed the same behavior in the South African *Leptogenys stuhlmanni*: "It appears to feed exclusively on wood-lice; the entrances of the nest can be plainly distinguished by the accumulation of the remains of their prey, bleached a dead white, scattered about it." More recently Illingworth and F. X. Williams have observed that the Hawaiian *L. falcigera insularis* feeds similarly on Oniscids (*Philoscia angusticauda*). I have shown (1933), however, that the West Australian *Lobopelta neutralis* feeds mainly, at least during the breeding season, on the queens of various ants, and especially those of a variety of *Crematogaster* (*Orthocrema*) *dispar*. Mann (Wheeler and Mann, 1914) observed a worker of the Haitian *Emerylla schmitti* "carrying a Polydesmid Diplopod thrown over its body in such a manner that the ant was entirely concealed beneath its burden," and he adds: "Scattered about in the nest were numerous fragments and several entire examples of a species of Polydesmid and of another Diplopod allied to our northern Julus. This fact, together with the behavior of the worker described above, indicates that *E. schmitti* feeds chiefly or entirely on Myriopods." The food of the South African *Plectroctena mandibularis*, according to Arnold (1915) "includes termites but consists chiefly of Diplopod millipeds and beetles," and that of *Platythyrea arnoldi* "consists entirely of beetles, mostly Tenebrionidae." He describes the nest of this ant as "surrounded exclusively with the remains of beetles." Dr. C. P. Haskins informs me that the most primitive of our North American Ponerinae, *Stigmatomma pallipes*, which he has been observing for many years both in the laboratory and in the field, preys exclusively on Geophilids, a group of very long, slender Chilopod Myriopods, known to feed on earthworms.¹ The dependence of *pallipes*, which is a subterranean ant, on such neither very abundant nor easily captured prey as the Geophilids probably accounts for its restriction to a narrow, undisturbed, forest environment, as I noticed in one of my earliest myrmecological papers (1900). In all the Ponerines cited in this paragraph the workers forage singly and not in troops like the species of Termit-

¹ The Germans call the Geophilids "Erdläufer." "They are," writes Verhoeff (1925, p. 28) "completely blind and therefore avoid the light. Probably most of the Geophilids prey on earth worms, which they embrace like snakes and gradually overcome by means of the poison from their jaws and ventral glands, while their body with its many muscular legs terminating in sharp claws is applied to the worm's body like barbed wire."

topone and the Old World termite-raiding Ponerines described in the sequel.¹ The Ethiopian and Indomalayan Regions, in which the termites exhibit such a remarkable diversity of forms and abundance of individuals, are, as we should expect, the very regions in which we find the most spectacular termitophagous ants. Arnold (1915) is therefore justified in his contention that "the economic value of the Ponerinae in tropical countries can hardly be overestimated, for it may be safely asserted that at least 80 percent of their food consists of termites, and they thereby constitute one of the chief checks to these pests in the tropics."

The most conspicuous termite-raiders in the Ethiopian region are three large, black species, *Megaponera foetens* Fabr., *Paltothyreus tarsatus* Fabr. and *Ophthalmopone ilgi* Forel. *M. foetens* (Fig. 4), especially, which is distributed throughout Africa south of the Sahara is one of the most remarkable ants. Its raiding columns, which sometimes number more than 1000 individuals, have been observed by a number of explorers and entomologists—Livingstone (1859), Sjöstedt (1905-'06), Wellman (1908), Prell (1911), Bequaert (1913), Alluaud and Jeannel (Santschi, 1914), Arnold (1914, 1915), G. D. H. Carpenter (Poulton, 1916), Lang (Wheeler, 1922), Ghesquière (1922), Schouteden (1924) and Collart (1925, 1927)—and will undoubtedly attract the attention of many more. References to or quotations from most of these writers will be found in my account of the ants of the Belgian Congo (1922) and in Hegh's volume on the termites (1922). Here I quote Arnold's succinct account from the introduction to his "Monograph of the Formicidae of South Africa" and some passages from Ghesquière's and Collart's more recent papers. According to Arnold, *M. foetens* "marches in double file and the striking disparity in size between the two forms (majors and minors) composing the colony has a very singular appearance. Their prey consists entirely of termites, and when a suitable hunting-ground containing these animals has been found the columns break up and pour into every hole and crack which leads to the invaded galleries. The method then adopted is as follows: Each ant brings to

¹ Probably certain members of the very primitive subfamily Cerapachyinae, formerly regarded as Ponerines, are termite-raiders. That some of them are specialized feeders is indicated by the Australian species of Phyracaces, the only genus of which the foraging behavior has been observed. Clark (1925) and I (1918) have shown that they are not termitophagous but attack colonies of other ants and carry off their brood. The hunting parties of Phyracaces, however, march in files like those of *Termitopone laevigata* and, except in their fewer numbers, resemble those of the driver and army ants (Dorylinae).

the surface one or more termites, and then re-enters the galleries to bring up more victims. This is continued until each ant has retrieved

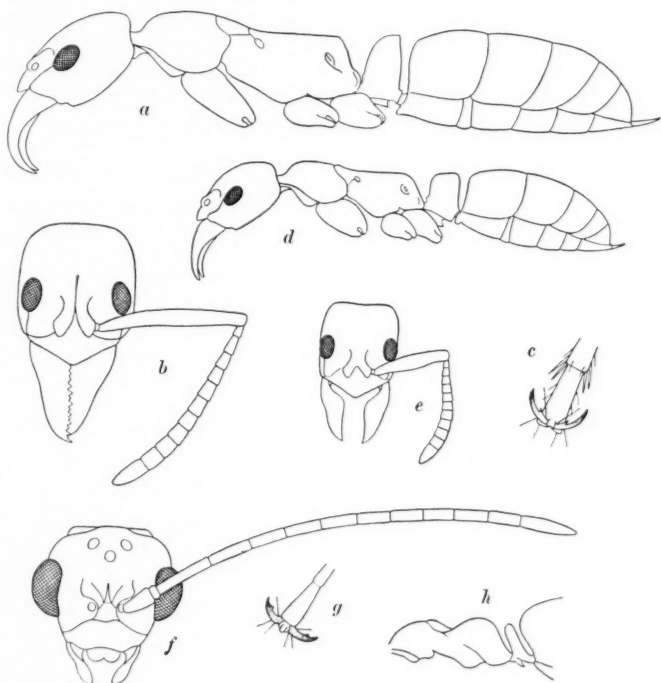


FIGURE 4. *Megaponera foetens* (Fabr.). *a*, worker major, in profile; *b*, head of same, dorsal view; *c*, last tarsal joint, showing the toothed claws; *d*, worker minor, in profile; *e*, head of same; *f*, head of male, dorsal view; *g*, last tarsal joint of same; *h*, thorax and petiole of female, in profile, after G. Arnold.

about half a dozen termites, which, in a maimed condition, are left struggling feebly at the surface. The whole army reassembles again outside, and each marauder picks up as many termites as it can conveniently carry, usually 3 or 4. The columns are then re-formed and march home." Ghesquière, who observed *M. foetens* in the Belgian

Congo, found that quite a number of its workers are maimed or wounded by the termite soldiers and that the combat between these and the invading ants "lasts at most thirty seconds. The column reforms rapidly and moves off in the direction of its nest, approximately over the same route as that of its outward journey. More than 80 percent of the ants carry prey, i. e. termite soldiers, workers and nymphs. The wounded ants follow the column with difficulty and one observes that the laggards are four or five meters in the rear. Many of them, nevertheless, carry prey. After a combat there are 4 to 5 percent wounded. When on their return the combatants arrive within a few decimeters of their nest, the guardians of the latter begin to show signs of excitement, but, after some hesitation, recognize the arrivals, which disperse and hurry into the formicary. The wounded ants, too, arrive and whether with or without prey are permitted to enter, but soon afterwards are evacuated and transported by the workers to a distance of about twenty meters from the formicary. If the wounded ants again return, the guardians forbid their entrance. The *Megaponeras* also have individuals that explore singly."

M. foetens, apart from its extraordinary raids on termites, also exhibits a number of other peculiarities. Thus several of the observers have called attention to the loud, sibilant stridulation of its marching columns. Santschi (1927), in support of the view that this stridulation, which is said to be audible at a distance of several meters, is "both a signal of alarm and a means of rallying the individuals," cites Collart (1925), who observed that the army while on the march "is led by a single individual, the ant-guide, who precedes the column but may be for brief periods surpassed by some of her companions. If the ant-guide be removed, the whole army halts, hesitates for some time and then with decision takes the road back to the nest. This fact is said to be well-known to the aborigines." Santschi adds that Collart, "having buried a worker *Megaponera* in the sand with his foot 50 cm. from the column, heard a faint stridulation and saw the whole mass of ants hasten to the succor of the victim and disinter her. Here, therefore, we have a recognition and a localization of a signal. The same factors may explain the behavior of the ant-guide and her followers." More recently Collart (1927) has described additional experiments that support his conception of the single guide on the outward bound razzias of *Megaponera*. "At Sanga, on September 29, from a column "on expedition," I carefully remove the ant-guide, at a moment when she is leading the others by several centimeters. As foreseen, when the column reaches the point at which I removed the guide, the

column halts. I wait till the whole column is assembled at that point, before throwing the ant-guide into the midst of the compact group thus formed. The insect remains stationary for a few moments as if stunned. Then she makes her toilet, brushing her antennae, while the others, after recognizing her without doubt, surround, palpate and caress her. When her toilet is completed the ant orients herself in the direction she was taking at the moment of her capture, makes her way through the column and resumes, without hesitation, the direction she was pursuing. Behind her the column re-forms. Again I withdraw the insect from the column and see the same behavior repeated. After having replaced the ant-guide in the midst of the group, the convoy re-forms. These experiments lead me to conclude definitively that during these raiding expeditions only a single ant knows the trail to the termitary that is to be pillaged. On the return to the nest, when the *Megaponera* are laden with prey, I may withdraw several of the ants marching at the head of the column, without preventing its normal advance towards its goal." This account of the behavior of the ant-guide is also supported by Ghesquière and Schoutedden, who, like Collart, repeatedly observed that columns on their outward march pass many termitaries without any attempts to plunder them.

Arnold (1914) has published an interesting account of *Megaponera*'s frequent changes of domicile, probably necessitated, as in the Doryline ants, by the need of ever fresh supplies of prey. He has also described the numerous myrmecophiles and synoeketes which as camp-followers accompany the armies on their migrations, together with the queen, which he describes and figures as a peculiar, wingless, ergatomorphic insect, measuring 18.5 mm. (Fig. 4 *h*). In connection with *Termitopone laevigata* (p. 160) I called attention to the clearly dimorphic workers of *M. foetens*. Arnold (1915) was the first to call attention to the differences between the two forms, after Gerstaecker had described the minor as a distinct species, *M. crassicornis*, and Emery had described the media as another species, *M. dohrni*. The minor worker (Fig. 4 *d-e*) differs from the major (Fig. 4 *a-c*) not only in its much smaller size but also in having the head and thorax much more shining and less pubescent, the antennal scapes shorter, the funicular joints transverse, the mandibles edentate and red and the dorsal surface of the petiolar node flatter and more horizontal.

A few observers have noted that *M. foetens* exposes its cocoons to the sun, a peculiarity of behavior which I described (1915) in certain Australian Ponerines (*Diacamma* and *Rhytidoponera*). Apparently

the thick, leathery consistency and black or dark brown color of the cocoons of these ants and *M. foetens* protect the enclosed delicate prepupae or pupae from injury by the ultra-violet rays. Mr. H. O. Lang, without knowing of my observations on the Australian Ponerines, informed me that he had seen *M. foetens* often exposing heaps of its dark cocoons to the sunlight, and more recently Schouteden (1924) has commented on this peculiar behavior: "Megaponera also has a habit, exceptional among ants, of frequently exposing the nymphal cocoons of the nest to the light. And you will thus have occasion to see a series of brown cocoons on their nests, fully exposed to the sun and guarded by sentinels."

Paltothyreus tarsatus, which, as we have seen, was confused by Latreille with the South American *Termitopone commutata* forms much smaller colonies than *M. foetens*. Arnold describes its troops as less orderly and says that he has "often seen this ant carrying termites, in short single files composed of about a dozen workers." According to Ilg's observations, published by Forel (1923), the termite raids of *Ophthalmopone ilgi* in Abyssinia are very similar to those of *M. foetens*. Arnold has found another species, *Ophthalmopone berthoudi*, nesting in deserted termite mounds in South Africa.

Both in the Ethiopian and Indomalayan Region there are several Ponerines of the genus *Leptogenys* and especially of its subgenus *Lobopelta*, which are known to be obligatory termite-raiders. According to Arnold (1915), the African *Leptogenys schwabi* "is crepuscular or nocturnal, and preys on termites." It is not stated that this ant raids in files. Some species of *Leptogenys sens. str.*, however, are able to adopt this formation. I have seen a dense single file of about 150 workers of a large, undescribed *Leptogenys* moving along a trail on Barro Colorado Island. This was not a raiding party, but a migration to a new nest, because the ants were carrying their brood tucked under their bodies in the Ponerine fashion. In the Oriental Region termite-raiding by well-organized armies has been observed in at least seven species of *Lobopelta*, namely, *aspera* Ern. André, *binghami* Forel, *birmana* Forel, *chinensis* Mayr, *diminuta* F. Smith, *kitteli* Forel and *processionalis* Jerdon. Though Rothney (1889, 1895) saw the marching armies of *chinensis* and *diminuta* in India, he says nothing about their prey, but Wroughton (1892) quotes the following observations of Aitken on *chinensis*: "There is a populous community of this ant, in a hole, in the foundations of my house at Goa. From the nest there is a well-marked 'road,' crossing a broad gravel path, and then ramifying all over the tennis ground. They issue after

sunset, and march along one of the main branches, or break up into parties and take different routes. When they come to a place where the termites have thrown up new earth-works, and are busy eating the dead grass underneath, they collect in dense masses, waiting for an opportunity to break in, which they very likely find when the termites attempt to extend their works on any side. Then the slaughter begins. Sometimes the poor termites are killed far faster than they can be carried off; and on one occasion, as late as 7 a.m., I saw the ground still heaped with slain, and an unbroken stream of ants, 56 yards long, carrying them away. Each ant had two or three in her jaws." Concerning *distinguenda* (= *processionalis*) Wroughton writes: "*L. distinguenda* may sometimes, it is true, be found loafing about singly, but these individuals are probably only scouts; ordinarily, she is only met, in the early morning or late in the afternoon, travelling in an unbroken column 4 to 6 or 8 abreast, straight, or by the easiest road, to the scene of operations. This is usually a colony of white ants whose galleries have been broken open by the hoof of a passing beast, or some similar accident. Arrived at destination, each worker seizes her termite prey, tucks it under her thorax in the orthodox ponerine fashion, and the column then returns (but marching 'at ease' and much less regularly than on the outward journey) to the nest." Bingham (1903) observed the raids of five of the above mentioned *Lobopelta* species in Burma and found that *chinensis*, *birmana* and *kitteli* seem always to march in columns of four, while *binghami* and *aspera* were seen "in single or double file, and very often singly, wandering about foraging, like *Diacamma*." He confirms "Mr. Wroughton's observations as to the termitophagous habits of this genus."

More recently (1911), Escherich has witnessed the razzias of *Lobopelta processionalis* in Ceylon. "Everywhere and every day," he says, "I could see their endless armies filing across the roads and along the waysides, most of the ants laden with dead termites or termite nymphs. And when I was opening mounds, I found them streaming in orderly columns into the exposed galleries and chambers to rob and plunder with all their might, as described by Wroughton. Whether these colonies had their nests (like the colonies of *Odontomachus*) in the particular mound I was excavating or only in the vicinity and were attracted by the opening of the galleries, I was unable to ascertain. The arrival of this readily stinging ant interfered so much with my work that I hastened to leave the mound as soon as possible."

It is very probable that several other species of *Lobopelta* which form populous colonies, such as *iridescent* and *mutabilis* of Indonesia and *fallax* of Queensland, have similar habits. I surmise, also, that this is true of the three known species of *Onychomyrmex*, a genus peculiar to Australia. These ants form populous colonies each with a single apterous, ergatomorphic queen like the colonies of Oriental and Australian species of *Lobopelta*. *Platythyrea* is another genus of termite-raiders. With the exception of *P. arnoldi*, mentioned above, most of the African species are, according to Arnold, "eminently termitophagous." The Neotropical forms are rare and almost nothing is known of their behavior, but I suspect, from a few casual observations, that they are termitophagous like their larger and more numerous African congeners.

The facultative termite-raiders may be subdivided into those that feed extensively on termites and those that have other important food-sources and prey on termites only occasionally when termitaries in their immediate neighborhood have been accidentally broken open or when a dispersion flight of the winged males and females occurs. At such times the foraging ants, like many species of birds and lizards and some social wasps, hasten to avail themselves of the nutritious bounty. No useful purpose would be served at the present time when we know so little about the normal food of most tropical ants, by citing observations recorded in the literature or in one's notebooks. I shall therefore close this section with a brief account of a few African and Australian ants that seem to feed largely on termites.

We should expect the army ants (*Eciton*) of the New World tropics and the driver ants (*Dorylus*) of the Old World tropics to raid termitaries just as they raid the nests of ants and capture all sorts of insects. It is doubtful, however, whether the *Ecitons* eat termites. While I was collecting at Kartabo, British Guiana, I had the impression, which was shared by other workers at the laboratory, that the *Ecitons* avoided the termites.¹ This does not seem to be true of

¹ These remarks are supported by the following unpublished observations generously contributed by Dr. Emerson: "Kartabo, British Guiana. Nests containing *Nasutitermes* (*N.*) *costalis* (Holmgren) were placed at different times in army ant (*Eciton*) trails. The ants definitely avoided the nest and reconstructed their trail around it. Once a trail of army ants (a species from which many guests were taken and determined by Wheeler as *Eciton burchelli* Westwood) entering a hollow tree to their nest, crossed a covered passageway of *Nasutitermes* (either *costalis* or *ephratae*). Upon my opening the passageway, the entire march of the army ants was stopped, none of them crossing the half inch space which was occupied by a few termites. Later on the ants

the African Doryli, though there are very few observations on their attacking termites. Hegh cites only two, one by Luja, who saw armies of *Dorylus (Typhlopone) fulvus dentifrons* Wasmann pillaging termitaries of *Acanthotermes spiniger* Sjöstedt in the Belgian Congo, and one by Buchholz who witnessed the pillaging of a termitary of *Basidentitermes aurivillii* Sjöstedt by *Dorylus (Rhogmus) fimbriatus* Shuckard in the Camerun. More important as a termite-raider is the Ponerine *Euponera (Brachyponera) sennaarensis* Mayr, which has a wide distribution over the whole Ethiopian Region and extends even into Arabia. According to Arnold (1914), "the economic value of this little species can hardly be overestimated, since it is exceedingly plentiful and preys unceasingly on termites. It is, however, omnivorous since it will eagerly collect bread-crumbs, insects of all sorts, and grass seed. Heaps of the latter are often found in the nests." A closely related species, *E. (B.) lutea* Mayr, is abundant throughout Australia and seems also to be highly termitophagous, but does not collect seeds. Other species cited in the literature as frequently feeding on termites are the Argentine ant, *Iridomyrmex humilis* Mayr,

found a roundabout way of entering the hollow tree without crossing the broken passageway.

"On another occasion in 1920 I placed a bit of wood containing workers and soldiers of *Coptotermes testaceus* (L.) in an army ant trail. The ants did not attack the termites for about 10 minutes, but finally a worker termite was carried off.

"Barro Colorado Island, Canal Zone, July 19, 1935. *Eciton (Labidus) praedator* F. Smith (det. W. M. Wheeler) did not attack trails of *Nasutitermes columbicus* on ground with which they came in contact and were repelled immediately by *columbicus* workers and soldiers placed in their midst. When 10 workers and 10 soldiers were taken from the trail and placed in the trail of the ants, the ants bit the termites but did not carry them away as they did other insects such as a roach. The soldier termites repelled the ants with the frontal gland secretion.

"Such avoidance of termites by *Eciton* contrasts with the readiness with which other ants attacked termites when their nests were broken open or when the termites were moving in open trails on the ground. *Pheidole fallax* Mayr (det. Wheeler) was seen carrying a minor soldier of *Rhinotermes hispidus* Emerson. *Gigantiops destructor* is reported by Wheeler (1922, p. 189) as attacking termite workers. *Neoponera apicalis*, *Ectatomma quadridens* and *Pheidole biconstricta* (det. Wheeler) were found preying upon an open trail of *Syntermes territus* Emerson. *Anochetus (Stenomyrmex) emarginatus* Fabr. (det. W. M. W.) was found preying upon a worker *Nasutitermes* sp. *Ectatomma tuberculatum* Olivier (det. W. M. W.) was found with a soldier of *Nasutitermes (N.) acajullae* (Holmgren) in its jaws."

in New Orleans, *Monomorium salomonis* L. and *Solenopsis geminata rufa* Jerdon, in India, and the South African *Xiphomyrmex weitzaeckeri* Emery, which, according to Arnold (1916) "preys to a great extent on termites, and also attends aphides and scale insects on plants."

Finally, there are also subterranean ants that feed on subterranean termites. The types of the Australian *Machomyrma dispar* Forel (1895) were taken by Gilbert Turner in actual warfare with a colony of these insects. *M. dispar*, like its closest allies of the genus *Pheidole*, has minute, yellow workers and much larger, large-jawed and aggressive soldiers, which must be more than a match for the termite soldiers. I believe that the very similar *Anisopheidole froggatti* Forel, which I have observed in West Australia, must have very similar habits. Its colonies, which may be very populous and comprise not only minute, pale yellow workers and huge, red-headed soldiers but also intermediates of all sizes between these two castes, nest deep in the soil or under large stones. It is difficult to see how this ant can develop such populous colonies unless it has an abundant food supply such as only termites or perhaps the broods of other ants would provide.

2. CLEOPTOBIOSIS

This term, as restricted by Forel (1901), is now applied to "those cases in which small ants establish their nests near or on the nests of larger species and either feed on the refuse or waylay the workers when they return to their home and compel them to give up their booty (Wheeler 1910)." Behavior of this pattern is exhibited by several small Dolichoderines, such as the European *Tapinoma erraticum*, the American *Iridomyrmex analis* Ern. André, *Forelius maccooki* Forel and *Dorymyrmex pyramicus* Roger, and by an Indian *Crematogaster*, the workers of which, according to Wroughton (1891), "lie in wait for *Holcomyrmed*, returning home, laden with grain, and by threats, rob her of her load, on her own private road, and this manoeuvre was executed, not by stray individuals, but by a considerable portion of the whole community."

One of the known cases, in which termites are concerned in a cleptobiotic relationship was witnessed by Ghesquière (Hegh 1922). In a passage quoted above (p. 184) he claimed that attacking *Megaponera foetens* workers are not infrequently wounded by the soldier termites. He also observed that the singular Myrmicine ant, *Atopomyrmex mocquersyi* Ern. André, is fond of termites, but instead of attacking them directly, assaults the wounded *foetens* workers and

robs them of their prey. In the combats which he witnessed between *Atopomyrmex* and maimed *Megaponeras* the latter were rarely victorious. *A. mocquerysi*, a solidly built, slow-moving ant, represented by several subspecies and varieties in the Ethiopian Region, nests in cavities in dead wood and is chiefly carnivorous, though both Ghesquière and Bequaert have seen it sucking nectar from flowers.

A species of *Myrmecaria* (unidentified, but probably some form of the common Ethiopian *eumenoides* Gerstäcker) also endeavors to wrest the termite booty from homeward-bound *Megaponera* workers. Collart (1927) saw "at Sanga (in the Belgian Congo) a column of *Megaponera* returning from a raid pestered by *Myrmecarias* which tried to rob them of their termites." . . . "This was the second time I was privileged to witness such a spectacle. Previously, in fact, at Kimuela, I had seen these same *Myrmecarias* annoying a group of *Megaponeras* while they were quitting the termitary they had pillaged. Moreover, on the day after my observation at Sanga I saw several *Myrmecarias* join a *Megaponera* column, but at the end of the procession, after all the booty-laden ants had passed. It was a curious spectacle to see the *Myrmecarias* hurling themselves at the powerful mandibles of the ponerines, which obligingly halted and submitted to the encounter. More than once I surprised a *Myrmecaria* poised on the head of a halted *Megaponera* and after quitting this position climbing onto another ponerine." In no instance, apparently, did Collart actually witness the seizing of the prey, but the behavior of the *Myrmecarias* seems to be unintelligible unless they at least occasionally succeed in robbing the *Megaponeras*.

3. TERMITOLESTY

This term was first applied by Forel (1901) to the cases of surreptitious predatism exhibited by certain "thief-ants," which have minute, pale yellow, blind or myopic workers that nest in the interstices or partitions of the nests of other larger ants or of termites and devour their brood. We may therefore distinguish two kinds of thief-ants, the myrmecolestic and the termitolestic, according to their preference for nesting in formicaries or in termitaries. The workers gain access to the nurseries of their hosts through very tenuous galleries which they excavate in the partitions. Thus protected from invasion of their own nest by the bulkier hosts and provided with a rich and abundant supply of food, the thief-ants are able to rear very large, winged males and females, with well-developed eyes and often deeply

pigmented integument. This lestopibiotic behavior, which was at first regarded as a peculiar relationship of certain ants to other ants (myrmecolesty) was discovered by Forel (1869, 1874) in the common European *Solenopsis fugax* Latreille and described, when he was only twenty-one, in the first of his many contributions to myrmecology. His results were later confirmed by Wasmann (1891) and Janet (1897). I insert a portion of the latter's interesting account of this ant: "Wasmann (1891, p. 21) mentions an extremely populous nest (*of fugax*) provided with some twenty queens and extending in a semicircle around the subterranean portion of a *Formica pratensis* nest, with which it communicated by means of fine pillaging galleries. Forel and Wasmann, however, have also met with isolated nests. At Beauvais I was able to ascertain, by following carefully during several hours the spading of a piece of land with southern exposure, left fallow for several years and almost devoid of stones, that the nests of *Solenopsis* may often be isolated, or at least noticeably distant from the nests of any other species. Nevertheless, this distance does not at all preclude the possibility of a communication by means of long galleries with the ant nests of the neighborhood, e. g. with those of *Tetramorium*, which were not rare in the same piece of ground. It is probable that the *Solenopsis*, when necessary, manages to go a considerable distance in search of the ant pupae that appear to constitute its principal food, but there is, nevertheless, a propensity to settle near the nests which furnish this food, and this approach is favored by the presence of stones, under which ants have such a pronounced tendency to shelter themselves . . . In the sandy soil of the piece of land above mentioned I obtained some fine and very clear vertical sections of the nests of *Solenopsis*. They consisted of small chambers of a circular form measuring 8-20 mm. in diameter and only 6-8 mm. in height. Most of these chambers were at least several centimeters apart. Their floors were remarkably clean, smooth and even hardened. They were connected by tenuous galleries, often less than 2 mm. in diameter, entering the chambers at their ceiling, at their lateral walls, or at their floors, and uniting with their surfaces by means of a perceptible infundibular orifice. Forel (1874, p. 385) saw several *Solenopsis* leave the earth and steal in among a stack of cocoons which had been heaped up by some *Formica pratensis* that he had dumped on the ground. The *Solenopsis* set to work perforating the cocoons and cutting the pupae to pieces, thus destroying a great number of them. Forel is correct in his inference that the *Solenopsis* behave in the same manner in double nests. At this writing I repeat

this observation daily on an artificial double nest of *S. fugax* and *F. rufibarbis*. Every day I give the *Solenopsis* about ten cocoons of *Lasius* queens, placing them near the entrance of the nest. It is not long before the *Solenopsis* make their appearance. From ten to thirty of them climb up onto each cocoon and cover it with little perforations, which, finally coalescing, enable them to reach its contents. If it contains a pupa, the legs and antennae fall an easy prey to the mandibles of the *Solenopsis*. In this case the victim is pierced, sucked, and torn into very small bits, which the ants hasten to carry away into the interior of their nest. The operation is much more difficult if the content is a larva which has just spun its cocoon, or a pseudonymph. I have seen the *Solenopsis* drag a larva of this kind into the interior of the nest and keep working at it for twenty-four hours. At the expiration of this period the larva began to look flaccid and was covered with little black dots, which were sometimes double, corresponding with the little wounds made by the mandibles. Numbers of the *Solenopsis* were busy lapping up the liquid which exuded from the wounds, but it was not till thirty-six hours had elapsed that the larva was entirely devoured. Large species of ants are unable to enter the nests of their neighbors, as the galleries of the latter are too narrow; and when the two species happen to meet one is inclined to believe, with Forel (1874, p. 246), that the small size of the *Solenopsis* renders them invisible to the larger ants. Then, too, in case of a conflict, the *Solenopsis* are numerous enough and sufficiently well-armed with stings to kill even *Formica sanguinea*. In my double artificial nests I often saw one of the latter killed by a group of five or six *Solenopsis*, but on such occasions I also found a considerable number of *Solenopsis* cadavers on the refuse-heaps."

Our widely distributed North American *Solenopsis molesta*, which is closely related to the European *fugax*, exhibits very similar behavior so far as its predilection for nesting in the formicaries of other ants is concerned (Wheeler 1901). Nor is it infrequently found in the nests of our subterranean termites of the genus *Reticulitermes* (*flavipes* Kollar, *lucifugus* Rossi and *virginicus* Banks). In the Southern states an allied, paler species, *S. texana*, has similar habits. The types of two of its subspecies, *carolinensis* Forel and *truncorum* Forel, were taken by Forel in North Carolina in termitaries.

Forel found that *fugax* sometimes nests independently, that it may prey on insects other than ants and that it frequently keeps root-aphids in its nests. It has not been sufficiently emphasized in the myrmecological literature that *lestobiosis* is only one aspect of a

much richer behavior pattern in this ant, since lestopiosis represents only one of its alimentary specializations. *S. molesta* seems to be even more versatile than *fugax*. Not only does it frequently nest independently both in the field and in houses, and cultivate a variety of root-coccids and root-aphids, but it has also a pronounced appetite for the softer portions of seeds. All of these habits have been described in detail in a comprehensive paper by Hayes (1920). He shows that the damage which *molesta* causes by eating into the recently planted seeds of gardens and especially the damage to seeds of sorghum and maize over thousands of acres in Kansas is so great that we are justified in regarding it as a serious pest. Hayes admits, however, that *S. molesta* is also beneficial and gives a list of a dozen of our pernicious insect pests on which it has been seen to prey. Of the interesting facts cited in the less economic parts of his paper only a few may be mentioned, e. g. the feeding of the *molesta* larvae by the workers both with regurgitated liquid food and small pieces of seeds, the size of the colonies, which, though highly variable in population, may comprise as many as 1300 to 1400 workers, and his list of some thirty species of ants and termites with which *molesta* has been observed to form compound nests.

That the minute species of *Solenopsis* may exhibit other unsuspected idiosyncracies of behavior is shown by Dr. Emerson's unpublished observations on *S. laeviceps* Mayr, which he encountered on two occasions in termitaries of *Nasutitermes* (*Constrictotermes*) *cavifrons* (Holmgren) at Kartabo, British Guiana. On the first occasion, July 20, 1920, the *Solenopsis* was nesting in some cells at the bottom of the termitary and had collected between 75 and 100 of the termites' eggs. The worker ants must have stolen these eggs from their hosts—probably not a difficult task for such diminutive and stealthy creatures. On the second occasion, March 10, 1924, the termitary had been abandoned by its builders and was partially occupied by a colony of *Nasutitermes costalis* Holmgren. In the bottom of the structure the *Solenopsis* were nesting in the dry food-material and had stored among their larvae many termite eggs and a single Staphylinid beetle (termitophile) egg. Dr. Emerson watched the ants for some time in an open cell with plenty of termites walking about, without noticing any hostile behavior on the part of the latter. Nor did the ants show any "fear" of the termites, although a colony of a small black *Crematogaster* (*C. limata* F. Smith), which was living in the dry food material of the same termitary "was attacked by the termites whenever they met. The termites were hostile even toward the larvae and were seen biting and chewing them."

The great increase of our knowledge of the tropical faunas during the past four decades has led to the recognition of a considerable number of ants possessing much the same structural peculiarities as the species of *Solenopsis* and nesting in the same manner with other ants and especially with termites. Although in most instances nothing further is known concerning these ants, it has usually been assumed that they are lestopibiotic. It seems advisable, however to relegate many of them to our category of inquilines and, at least for the present, to regard as lestopibiotic only those that are taxonomically most closely related to *Solenopsis*. As thus restricted the lestopibiotic species belong to only two of Emery's Myrmicine tribes, the *Solenopsidini* and the *Pheidologetini*, which are so closely interrelated that there is doubt as to whether they should not constitute a single tribe. Forel was of this opinion, but Emery regarded them as distinct but convergent series, differing mainly in the open (*Solenopsidini*) or closed (*Pheidologetini*) radial cell of the wings. All the species of both groups have minute and either blind or myopic workers and comparatively large females and males, but most of the *Pheidologetini* have in addition to the diminutive worker proper a larger, huge-headed, soldier caste. Several of the *Solenopsidine* genera (*Vollenhovia*, *Allomerus*, *Huberia*, *Phacota*, *Xenomyrmex*, *Megalomyrmex*, *Epixenus* and *Wheeleriella*) and the genus *Pheidologeton* are certainly not lestopibiotic, but the following fifteen genera contain species which are probably more or less addicted to that type of behavior:

Solenopsidini: *Solenopsis*, *Liomyrmex*, *Carebarella*, *Diplomorium*, *Anillomyrma*, *Tranopelta* and *Tranopeltoides*.

Pheidologetini: *Lophomyrmex*, *Trigonogaster*, *Oligomyrmex*, *Aëromyrma*, *Aneleus*, *Erebomyrma*, *Paedalgus* and *Carebara*.¹

Our knowledge of the tropical species of these various genera is still so meager that in most cases it is impossible to say whether a recorded form is more given to association with other ants or with termites. This is particularly true of the minute species of *Solenopsis* of the subgenus *Diplorhoptrum*, to which *fugax* and *molesta* belong, a subgenus which is represented by a great number of forms in tropical America. Four of the genera, namely *Tranopelta*, *Erebomyrma*,

¹ The minute, myopic species of *Monomorium*, *Anillomyrma*, *Lophomyrmex* and *Trigonogaster*, included in my list of termitolestic ants (Appendix A), may not belong to this category, but are, perhaps, hypogaecic forms that merely find optimal nesting sites in the earth or carton of termitaries. If this is the case, they should be ranked as inquilines and transferred to the list of Appendix B.

Paedalgus and Carebara, however, are of unusual interest because they seem to form a series in which the difference in size between the worker and female increases very rapidly, with a concomitant increasing tendency to termitolesty. I subjoin a brief account of each of these genera.

(1) *Tranopelta* comprises only three known species, all confined to South and Middle America. The females and males of the genotype, *T. gilva* are common at lights, and it was on these sexual castes that the species was based by Mayr in 1866. Forel, in 1908, described all three castes of a var. *brunnea* (= *amblyops* Emery) of this ant from Paraguay, and in 1920 I was able to take all the castes of the typical *gilva* in British Guiana. Whereas the female of *Solenopsis molesta* is only about 25 times as large as the conspecific worker, the volume of the *Tranopelta gilva* female is more than 70 times that of the worker. The following notes are transcribed from my taxonomic paper (1922) on *Tranopelta* and allied genera, in which the description of the worker was drawn from two colonies containing also many males and females. One colony was taken at Kartabo, August 3, 1920, while Dr. Alfred Emerson and I were excavating a large colony comprising more than 500 workers of the formidable stinging ponerine, *Paraponera clavata* Fabr. The *Tranopelta* were occupying small chambers one to one and one-half feet below the surface of the soil and communicating with the galleries of the *Paraponera*. In this case the smaller species was evidently behaving as a thief-ant. On August 1, I found the stomach of a four-toed ant-eater (*Tamandua tetradactyla*) to contain no less than 14 species of ants, a large proportion of which consisted of hundreds of workers and dozens of males and winged females of *Tranopelta gilva*. The ant-eater must have unearthed and devoured a very flourishing colony of this ant. July 15 I found at Barakara, on the right bank of the Mazaruni River, a large colony of *gilva*, comprising hundreds of workers but no sexual forms, under the bark of a living tree. On the surface of the wood the ants were attending numerous snow-white coccids which have been described by Dr. Harold Morrison as *Ripersia subcorticis*. Dr. G. H. Bünzli (1935) has recently found *gilva* attending root-coccids on coffee-plants in Surinam. There is nothing to indicate that this ant occurs with termites. Dr. Emerson, who has carefully studied the termites of British Guiana and has conscientiously preserved all the ants and other organisms which he has found with them, has never taken *T. gilva* in or near the nests. It would seem, therefore, that this species sometimes leads an independent life and that when it behaves as a

thief-ant prefers to associate with other Formicidae. *T. heyeri* Forel, the only other Tranopelta species concerning which we have any ecological data, was found by Heyer in Southern Brazil nesting in termitaries of *Eutermes fulviceps* Silvestri (= *Nasutitermes fulviceps*) and *Anoplotermes morio* Hagen (= *A. meridianus* Emerson). Its variety *columbica*, however, was taken by Forel in Colombia at the bottom of a nest of a small fungus-growing ant, *Mycocepurus smithi* Forel, and on a second occasion nesting independently under dried cow-dung.

(2) *Erebomyrma*, another neotropical genus, comprises only two known species, *E. longi* Wheeler (1903) of Texas, of which all the castes have been described and figured, and *peruviana* Emery, known only from a female specimen. The specimens of *longi* were captured by Mr. W. H. Long from a populous colony while they were issuing from the soil for the nuptial flight. The female is black, with blood-red abdomen and appendages and is about 150 times as large as the minute, blind, yellow worker. Since Mr. Long subsequently observed colonies of subterranean termites escaping for their dissemination flight from openings very near those from which the *longi* females, males and workers had issued, it is very probable that this species is termitolestic. Unfortunately, it has not been seen since 1903, so that we have no further data on its habits and distribution.

(3) The genus *Paedalgus* is known to comprise three species: *escherichi* Forel from Ceylon, *infimus* Santschi from French Guinea and *termitolestes* Wheeler from the Belgian Congo. Escherich discovered the Ceylonese species living in a small geode-like cavity in an *Odontotermes* (*Hypotermes*) *obscuriceps* termitary. The diminutive workers were running about "like lice or mites" on the body of the huge queen which was about 160 times as large as each worker. Santschi says nothing about the habits of *infimus*, which was collected by Silvestri, but there can be little doubt that the latter found the specimens in a termitary. *P. termitolestes* was taken by Lang and Chapin in a mound termitary of *Acanthotermes militaris* (Hagen). The colony, comprising many workers and their peculiar subspherical larvae, was nesting in cavities near the fungus-gardens of the termites. The workers, larvae and nesting site are figured in my "Ants of the Belgian Congo" (1922, Pl. 16 and text-figures 42 and 43).

(4) The species of *Carebara* are not only the most conspicuous of termitolestic ants but also exhibit certain other very interesting singularities of behavior. The genus comprises at the present time 15 species, of which two (*castanea* F. Smith and *lignata* Westwood) are

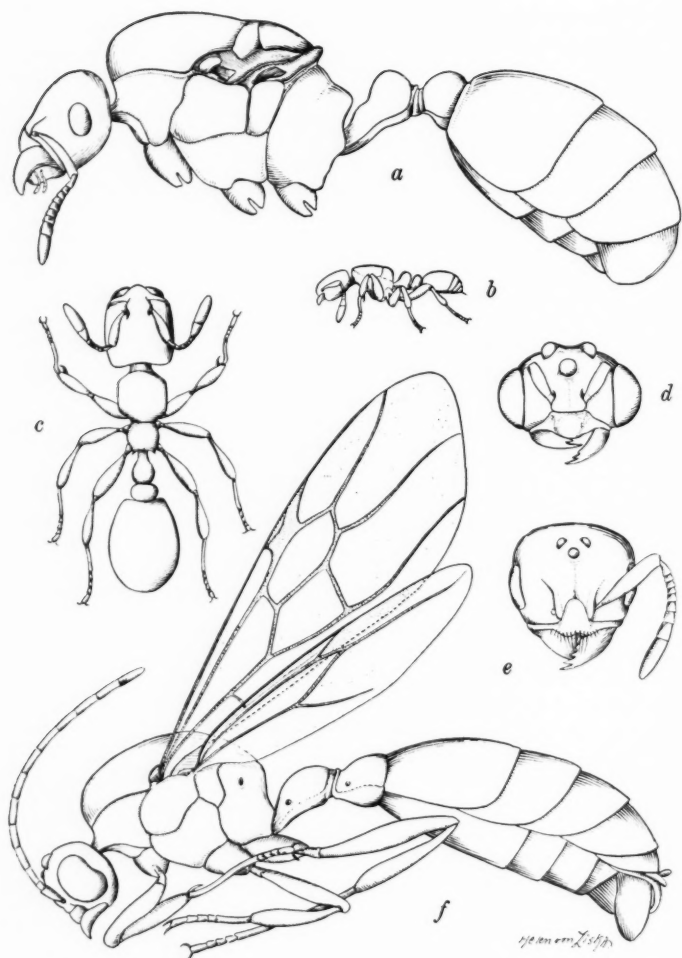


FIGURE 5. *Carebara osborni* Wheeler. *a*, deälated female; *b*, worker, drawn to same scale; *c*, same enlarged; *d*, head of male; *e*, head of female; *f*, male in profile; from *Termes natalensis* termitary, Belgian Congo.

Indomalayan, nine Ethiopian (*ampla* Santschi, *arnoldi* Forel, *junodi* Forel, *langi* Wheeler, *osborni* Wheeler, *sicheli* Mayr, *silvestrii* Santschi, *sudanica* Santschi and *vidua* F. Smith) and four South American (*anophtalma* Emery, *bicarinata* Santschi, *mayri* Forel and *winifredae* Wheeler). The difference in size between the workers on the one hand and the females and males on the other is much greater than in any other termitolestic ants but varies considerably in the different species. Thus the ratios between the worker and female in four of the species are very roughly as follows: *winifredae* 1 : 150, *osborni* 1 : 500 (Fig. 5) *lignata* 1 : 1000, *vidua* 1 : 2000 (Fig. 6). These ratios, however, are far too small because they were obtained by comparing the cubes of the lengths of the two castes, without allowing for their great differences in form, the female possessing large wings and a very much more voluminous head, thorax and gaster than the conspecific worker. The same statement applies, of course, to the ratios above cited for *Solenopsis*, *Paedalgus*, etc. Forel's method of comparing the weights of the two castes is much more satisfactory, but would yield accurate results only with living specimens.

It is interesting to note that the species of *Carebara* are associated only with the large species of the genera *Macrotermes*, *Acanthotermes* and *Odontotermes* of the family Termitidae, which build the huge mound termitaries in the Indomalayan and Ethiopian Regions, and with the allied species of *Syntermes* which inhabit extensive subterranean termitaries in South America. Of course, it would be impossible for such minute ants as the workers of *Carebara* to rear such enormous females and males unless they were able to draw on very populous colonies of large termites as a food supply. And not only are these ants able to produce such enormous sexual individuals but they are able to produce them in astonishing numbers as Dr. Bequaert (1913) has shown in the following account of a nuptial flight of *C. junodi*, which he witnessed in the Belgian Congo: "In the Katanga it lives in the mound-shaped nests of *Acanthotermes spiniger*. October 6, 1911, I witnessed at Sankisia a nuptial flight of this ant. It was the very beginning of the rainy season and on the two preceding days it had rained abundantly. Toward noon numerous winged females were flying about everywhere in the savannah; they came from a certain number of termitaria, the sides of which were covered with fabulous numbers of the very small workers of the same species. I did not see copulation but, in the evening, I captured several males at light but no females. The following days the phenomenon was not repeated. The huge *Carebara* females are, among the aborigines

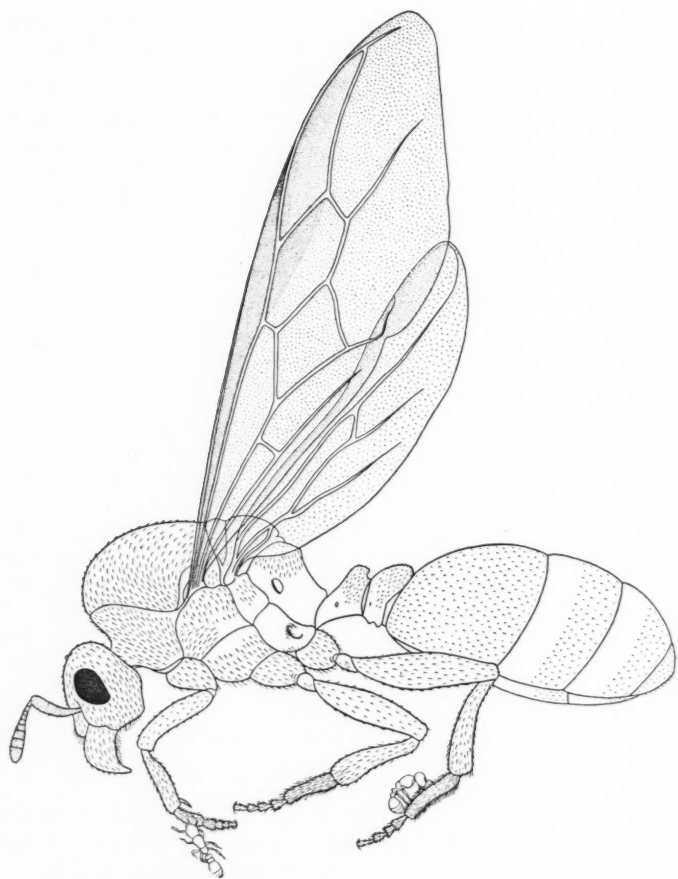


FIGURE 6. Winged, recently fecundated queen of *Carebara vidua* Haviland, carrying two minute, blind workers attached to her tarsal hairs.

of the Congo, a much sought-for delicacy. Hence they take advantage of the nuptial flight to collect a great number of individuals. The swollen portion of the abdomen alone is utilized. They eat it either roasted or raw!" Dr. Bequaert informs me that his attention was

directed to the marriage flight described above by the excitement of the congregated natives who were actually filling pails with the torn-off gasters of the females. Each Carebara colony gave off hundreds of females and the number of workers that covered a termitary during the flight must have run into the millions. The workers of Carebara, like those of other hypogaecic ants (*Erebomyrma*, *Acanthomyops*, etc.) apparently come to the surface of the soil only while the nuptial flight is in progress.

Although the founding of the Carebara colony by a single female has not been observed, there can be little doubt that immediately after her nuptial flight she excavates a small cell in a termitary near the chambers of the termites and lays a batch of eggs. The rearing of the minute larvae after hatching from the eggs, however, cannot be carried on by the same method of oral regurgitation as that employed by other colony-founding ants in which the difference in size between the female and her first brood of offspring is less excessive. The difficulties confronting the mother Carebara would seem to be like those of a mother hippopotamus trying to feed her offspring, if it were at birth only the size of a mouse, by placing the right amount of liquid food in its mouth. Arnold (1916) was the first to suggest a plausible solution of the problem in his account of *C. vidua*. He says: "It is probable that the dense tufts of hairs on the tarsi of the female serve an important purpose—that of enabling some of the minute workers to attach themselves to the body of the female when the latter is about to leave the parental nest. Several specimens of the female have been taken by me with one or more workers biting on to the tarsal fimbriae. I am inclined to suspect that the young queen cannot start a new nest without the help of one or more of the workers from the old nest, on account of the size of her mouthparts, which would probably be too large and clumsy to tend the tiny larvae of her first brood, and that it is therefore essential that she should have with her some workers which are able to feed the larvae by conveying to them the nourishment taken from the mouth of the queen." Often, indeed, the workers hold so firmly to the queen's tarsal hairs that they are preserved in this position in cabinet specimens (Fig. 6). I have found them attached also to the tarsi of the males. When this occurs in nature the workers must, of course, perish with their carriers immediately after the nuptial flight. There is some doubt about Arnold's inference that the workers transported to the new nest "are able to feed the larvae by conveying to them the nourishment taken from the mouth of the queen," since this nourishment could only

consist of regurgitated food and there is no reason to assume that the colony-founding queen leaves the parental nest with a supply of liquid food in her crop. It seems more probable that the transported workers either have to establish communication with the galleries of the termites and by preying on them secure the food with which to nourish the larvae or use some of the presumably numerous eggs of the queen as food for the initial brood. This rearing of a portion of the larvae by feeding them with some of the eggs or remaining larvae is commonly practiced by colony-founding ant-queens (see Wheeler, 1933), and no doubt instances will be found of workers resorting to the same expedient when their numbers are too few to provide an adequate amount of food from other sources.

Finally, attention may be called to an interesting analogy between the *Carebara* and termite queens. It is well known that in the very termites with which the *Carebaras* associate themselves, the queens, as a result of excessive feeding, assume enormous physogastric development during their adult instar. Similarly, the *Carebara* queen attains gigantic dimensions compared with the workers, though her excessive growth is exclusively larval. This peculiar parallelism or convergence on the part of the *Carebara* colony can be regarded only as due to the exceptionally favorable trophic and perhaps hormonal conditions that enable the termites themselves to produce such enormous queens (See Appendix C).

D. INQUILINISM

It is difficult to invent a name for the category including the large number of tropical ants that frequently occupy portions of the gallery system of inhabited or abandoned termitaries, without, however, clearly manifesting any such relations to the termites as those described above as termitolestic or those described in the sequel as termitoxenic. After inventing the term "synengyobiosis" and rejecting it as too awkward, it seemed best to employ the old term 'inquilinism' in the neutral sense of the German "Raumparasitismus." Since we have very little information concerning the precise relations of the great majority of inquiline ants to the termites, the category, as previously stated, is merely a classificatory makeshift and will be resolved eventually into a number of categories. This is clearly indicated by the fact that the ants which I assign to it differ greatly both in temperament and behavior. Some of them are extremely belligerent so that whenever the walls separating the galleries they have preëmpted from those of the termites are broken down, they at

once kill and carry them off, whereas other species are very pacific and under like circumstances merely desert their nest without paying any attention to the termites. Others, again, seem to resemble the termitolestic species or occupy abandoned termitaries simply because their galleries are sufficiently commodious or afford adequate protection from the inroads of other ants. In Appendix B I have given a list, compiled from the literature and unpublished records, of the forms which may be provisionally regarded as inquiline. Though undoubtedly incomplete, this list comprises a surprising number and variety of genera and species representing all but one (the *Pseudomyrminae*) of the eight subfamilies of Formicidae.

Even the ants of this category which are aggressive enemies of the termites, when they can gain access to them, show great differences in behavior. This will be apparent from the following account of three species.

In 1914 I noticed that in two types of earthen termitaries, one conical and the other broadly dome-shaped, in the vicinity of Townsville and Koah, Queensland, the basal or in some cases even the superficial galleries were very frequently inhabited by colonies of ants. The builders of the conical termitaries have since been described by Hill (1922) as *Hamitermes perplexus* (= *Amitermes wilsoni* Hill) and those of the domes as *Drepanotermes silvestrii*. I collected at least a dozen species of ants from these structures in the course of a few hours (Wheeler 1918). Most of them were inoffensive, but one, *Iridomyrmex sanguineus* Forel, like *I. detectus* F. Smith, the famous Australian 'meat-ant,' of which it has been regarded, erroneously I believe, as a mere subspecies, was extremely aggressive and annoying. What I saw of its behavior fully confirms the observations of Hill, who later made a more careful study of its behavior, and whose account I therefore quote at length. "At a very rough estimate it may be said that 80 percent of the termitaria of *D. silvestrii* and *H. perplexus* are invaded and permanently occupied by the very common and widely distributed ant, *Iridomyrmex sanguineus*, Forel, which is particularly abundant in the low-lying country in the vicinity of Townsville. The termitaria are entered by means of holes burrowed into the walls, in and out of which pass endless streams of ants in their journeys from one nest to another. If a termitarium is cut open vertically, it will be found that the ants have greatly enlarged the original galleries so as to form large flattened chambers in tier upon tier, until finally the greater part of the structure is in their undisputed possession. The floor of each cell is thickly covered with the eggs,

larvae and pupae of the invaders, and immense numbers of ants throng all parts not actually in possession of the termites. As the ants extend their sphere, the termites are driven back from chamber to chamber and destroyed, until but a few stragglers are left. The complete, or nearly complete, occupation of a termitarium is evidently a matter of time, during which the advance is being constantly delayed by the termites walling up their galleries and passages as they retreat. The remains of the dead termites in the chambers occupied by the ants show clearly that the nests are not attacked merely to provide a dry and safe shelter, but that the original occupants are used as food. Immediately the walls are broken with the pick the ants swarm out in countless thousands, destroying and carrying off the dislodged termites, crawling up one's legs and attacking one's hands, head or any skin surface to which they can gain access. Others of their kind gather from all directions to take part in the onslaught, until the nest and the surrounding ground is a seething mass of insect life. Under these conditions a close examination of the nest or its occupants is impossible, and it is only by finding an ant-free nest that one can hope to investigate the interior. Within a few minutes of the nest being broken into all the neighboring ant-infested termitaria of these two species will be found to contain the bodies of freshly killed termites, while files of ants pass to and fro so long as a termite remains exposed to attack. . . . It is a remarkable fact that the mounds of a certain species of *Eutermes* [= *Nasutitermes*], which are very common amongst those of the *Drepanotermes* and *Hamitermes*, are never molested by *Ididomyrmex*.¹

Fuller (1915) describes similar behavior in South African ants, though, unfortunately, he fails to identify the species. He found also that one species of termite, *Eutermes bilobatus* Haviland (= *Cubitermes bilobatus*) regularly dislodges another species, *E. trinervius* Rambur (= *Nasutitermes* (*Trinervitermes*) *trinerviiformis* (Holmgren)), only to be in turn dislodged by ants. The two termites are frequently associated, "*bilobatus* simply gaining an access to one point of the *trinervius* mound, and then by gradually converting the more open *trinervius* galleries into cells, it slowly builds the artificers out. This often results in the building of a new mound some little distance off by the *trinervius* community; in several instances this has been alto-

¹ This account shows that the adult colony of *I. sanguineus* is polycladic, or spread over several termitaries, unlike the *I. detectus* colony, which always occupies a single low mound nest that may have a diameter of several feet.

gether dislodged" . . . "It is scarcely possible to find a normal mound of *bilobatus* about Pretoria which has not a nest of a true ant in part of it; the ants capture the nest in the course of time by taking possession of it cell by cell. The process is not, however, a rapid one, as the termite can build up quicker than the ant can break down, and the very art which enables this termite to supplant another of its kind is its most potent means of defense where the ant is concerned. When a hive of *bilobatus* is broken into the ants excitedly swarm in at once and carry off the termites; they will not attack an injured nest of *trinervius* with like avidity and seldom make their own domiciles near to the mounds of this latter species. Indeed they evince great circumspection, and always endeavor to capture the *trinervius nasutus* from behind."

Anoplolepis (formerly *Plagiolepis*) *longipes* Jerdon, a very slender, long-legged, active ant, common throughout the Indomalayan Region and usually nesting in independent formicaries, is, according to Horn (Wasmann 1902) and Escherich (1911), a frequent inquiline in the mound termitaries of *Odontotermes* (*Cyclotermes*) *redemanni* Wasm. in Ceylon. Escherich found it in almost every termitary which he excavated, darting like a shadow over the breaches in order to secure the inhabitants. "But this is no easy matter for the breaches are at once manned by a cordon of soldier termites, which it is daring and foolhardy to attempt to break through. I was greatly astonished at the respect of the ants for the termites and especially for their soldiers. As soon as a *Plagiolepis* happened to touch one of the latter with the tips of its antennae, she started back in terror. They usually attempted to attack from the rear, and occasionally with success, so that here and there a termite worker or nymph was captured by resort to such tactics. In a few instances I saw a *Plagiolepis* dart like lightning through a cordon of soldiers, which had their mandibles directed to the outside like so many bayonets, and thus reach a gallery. Oftener a duel would ensue, ant and termite charging each other but at once retreating far from each other. After repeated charges of this kind the ant usually sank down impotently as if her limbs had been glued together. As a rule the termite soldiers were victorious but not infrequently they succumbed on the field of battle."

The number of inquiline ants in regions where mound-building termites abound is undoubtedly very great, and all myrmecologists who have carefully collected specimens from their structures in Southern Asia, Indonesia, Australia, tropical Africa and South America have made a rich harvest. Unfortunately, some termitologists

seem to be little interested in recording the ants which they must continually encounter while investigating termitaries. My lists (Appendices A and B) are made up mainly from the collections of

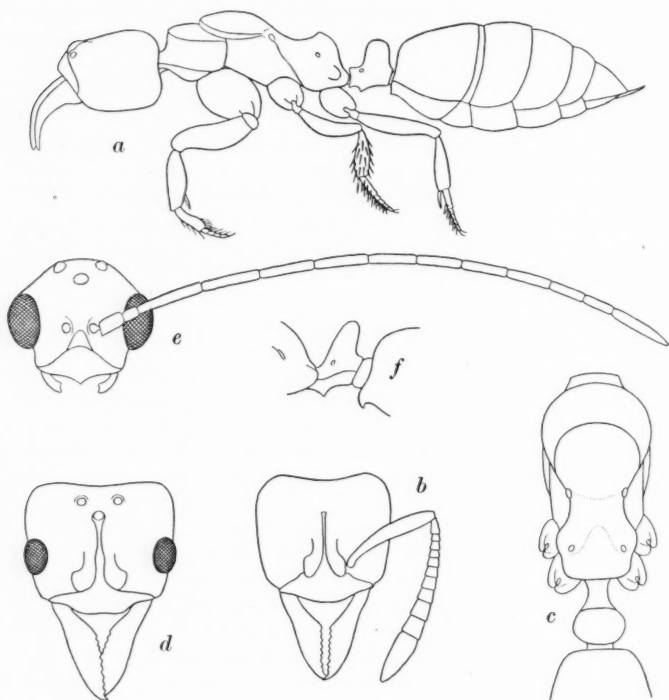


FIGURE 7. *Centromyrmex feae* (Emery) a, worker in profile; b, head of same, dorsal view; c, thorax and petiole of same, dorsal view; d, head of female; e, head of male; f, petiole of male in profile.

Bequaert (1913) in the Congo, of von Buttel-Reepen (Forel 1913) in Ceylon, Malacca, Sumatra and Java, of Dr. N. A. Kemner in Java, of Dr. W. Horn (Wasmann 1902) and Escherich (Forel 1911) in Ceylon, of Lang and Chapin (1922) in the Congo, of Schmalz and Heyer (Wasmann 1901, 1902, Forel 1895) in Brazil, of the species

taken in Australia by Mr. L. Glauert and myself and by Dr. Emerson and myself in British Guiana and Panama. Most of the recorded species have been taken only once and many of them are known to nest as a rule quite independently of termites. Others are rare forms which may be regular inquiline or have been found only in termitaries abandoned by their builders. A few have been collected so frequently in inhabited termitaries as to indicate definitive inquiline proclivities. A series of these may be singled out for special comment.

(1) *Centromyrmex feae* Emery (Fig. 7). This singular Oriental Ponerine, the worker caste of which (a-c) is eyeless and has peculiar, narrow, deflected mandibles, an unusual thorax, very spiny tibiae and tarsi and long, powerful forelegs, seems to be always associated with termites. Dr. Kemner sent me specimens from at least eight colonies together with their slender, tuberculate larvae and pale cocoons, all from termitaries of various Javanese termites, and Escherich (1911) had previously taken the var. *ceylonicus* Forel "always with termites" in Ceylon. H. von Buttel-Reepen (Forel 1913) found the typical *feae* at Malacca in the fungus-gardens of *Microtermes pallidus* Haviland. There can be little doubt that *Centromyrmex* feeds exclusively on termites, but whether it is termitolestic like *Carebara* and moves about unobserved among the termites, as indicated by von Buttel-Reepen's observation, or like the larvae of certain Carabid beetles (*Orthogonius*, *Rhopalomeles* and *Glyptus*) attacks the passing termites from the openings of its galleries as indicated by the shape of its mandibles and its powerful, spiny fore feet, or secures its prey in some as yet unsuspected manner, remains to be determined.¹

¹ Emery, in the "Genera Insectorum" (1911, p. 57), describes the male of the genus *Centromyrmex* as follows: "Head rounded, clypeus very convex (bombé). Mandibles very short, edentate. Antennae short. Thorax stout; mesonotum with Mayrian furrows. Petiole surmounted by a scale. Pygidium without a point. Spurs of median legs very small; medial spur of posterior legs pectinate." As there is no reference to a male in his list of the five described species of *Centromyrmex*, it is impossible to say which species furnished him with this generic description. Several males of *C. feae* taken with winged females and workers from the same colony by Dr. Kemner suggest that Emery's description may not be that of a male *Centromyrmex*. The male (Fig. 7 e, f) of *feae* measures 5-5.5 mm. It is black and pubescent, with piceous antennae and pale brown legs. The head is very small, the clypeus in the middle with a thick, anteriorly projecting tooth, the mandibles are very small but feebly bidentate, the antennae long and filiform, the thorax nearly twice as broad as the head, the mesonotum without notauli (Mayrian furrows), the pygidium terminates in a point, the genitalia are large for a male Ponerine; each middle tibia has a long, pectinated and a shorter, simple spur.

(2) *Dolichoderus (Monacis) laminatus* Mayr. In Panama this active, gentle ant seems to be a common lodger in the galleries of inhabited arboreal, "nigger-head" termitaries of *Nasutitermes ephratae* Holmgren. When the structures are broken open the ants escape very quickly without paying the slightest attention to the termites.

(3) *Opisthopsis haddoni* Emery. This very active member of an exclusively Australopapuan genus characterized by its huge eyes situated at the posterior corners of the head and thus enabling it to sense enemies approaching from the rear, nests almost exclusively in the clay termitaries of *Hamitermes perplexus* Hill [= *Amitermes wilsoni*], as will be seen from the following quotation from my monograph on the genus *Opisthopsis* (1918): "The interesting resemblance of these ants to the large-eyed, arboreal and bright-colored species of *Pseudomyrma* in the Neotropical and of *Sima* in the Palaeotropical region led me to look for their nests in the trees, but I failed in this quest and concluded that the nests must be at inaccessible heights in the trunks or branches. Through a fortunate accident, however, at Koah, near Kuranda, Queensland, I discovered the nests of one species, *O. haddoni*. In this arid forest region there are innumerable termite nests of all sizes from a foot or two to six or seven feet in height. I found that the smaller nests could be easily broken off at the base and turned over by a sharp kick with the foot. This exposed the galleries in the base of the termitarium and to my surprise I found most of them inhabited by a colony of the beautiful orange and black *haddoni*. Such study as I could make in the field showed that the ants take possession of the galleries by replacing the termites which retreat to the upper portion of the nest-cone. Perhaps the ants feed very largely on the soft-bodied termites, although the latter were not molested when they happened to creep into the galleries inhabited by the ants. From this and the further fact that I found *haddoni* nesting by itself under stones only on one occasion, I infer that this ant is regularly termitophilous. Later I again found *haddoni* nesting in precisely the same manner in termitaria near Townsville, Queensland. On my return to the United States I learned that Dr. E. Mjöberg (Forel 1915) had recently made similar observations on *O. haddoni* in the Kimberly District of North West Australia and at Laura, Cape York and Colosseum, Queensland." It now seems to me improbable that *O. haddoni* feeds on the termites. It is undoubtedly insectivorous, but like the other species of the genus, hunts on tree trunks and occasionally on the ground. Perhaps, also, the basal

galleries of the termitaries are abandoned by the termites before the ants take possession of them.

(4) *Calomyrmex*. The literature contains no account of the habits of this beautiful, exclusively Australopapuan genus. In 1914 I found a few very populous colonies of *C. albertisi* Emery nesting in mound termitaries of *Drepanotermes silvestrii* Hill at Koah, Queensland. The workers were foraging in long files. In 1931 I found numerous colonies of *C. splendidus purpureus* Mayr comprising about 300-400 workers and in some cases with numerous males and winged females at Mullewa, Meeketharra, Pindar and Yandil, in the dry zone of West Australia. In most of these localities the nests were in the soil under stones or quite subterranean with only a small circular opening on the surface, but at Pindar several colonies were found lodging in the lowermost galleries of conical termitaries very similar to those of *Amitermes wilsoni* in Queensland. *C. purpureus* does not forage in files. The workers of both species run about with the gaster conspicuously elevated and when seized with the fingers exude from the base of each mandible a minute drop of odoriferous, vermilion red liquid. Certainly *purpureus* is not a regular inquiline in termitaries and the same is probably true of *albertisi*.

(5) *Polyrhachis* (*Chariomyrma*) species. The conical termitaries of *Amitermes wilsoni* at Koah, Queensland frequently house in their upper galleries flourishing colonies of five different forms of this subgenus, namely *aurea* Mayr, *urania* Forel, *gab* Forel and two of its varieties, *senilis* Forel and *tripellis* Forel. Like all the numerous Australian species of *Polyrhachis* I have collected, these ants are timid and peaceable and none of them was seen to attack the termites when their dwellings were demolished.

(6) *Camponotus* (*Myrmophyma*) *rubiginosus* Mayr. This handsome red and black ant was taken in several *Drepanotermes silvestrii* termitaries at Koah, Queensland and was not found nesting elsewhere. It is a timid insect which builds on the surface of the termitary a small chimney-shaped structure with a circular orifice to serve as an entrance to the galleries it has preëmpted. This entrance is guarded by one of the large-headed major workers, which behaves very much like the soldiers of *Colobopsis*. Unfortunately, I find in my notes of 1914 no mention of the behavior of the ants towards the termites.

(7) *Camponotus* (*Myrmaphaenus*) *novogranadensis* Mayr. This ant ranges from Southern Brazil to Costa Rica and, according to my observations, very rarely nests independently. As will be seen from the records in Appendix B (p. 234), it has been taken in the termi-

taries of some four species of termites in Southern Brazil, British Guiana and Panama. Many of the termitaries of *Nasutitermes ephratae* which I examined on Barro Colorado Island and in other Panamanian localities contained colonies. The galleries usurped by the ants form a system which ramifies extensively among those inhabited by the termites. The colonies are rather small and even the larger workers are timid and peaceable, but when the termitary is demolished nevertheless attack and carry off the termites. Wasmann (1915) was the first to surmise that *C. novograndensis*, which Heyer found in termitaries of *Armitermes heyeri* Wasmann (MS) in the State of São Paulo, Brazil, is "perhaps to be regarded as a regular termite ant," because it resembles the following ant in size, form and opaque black coloration.

(8) *Camponotus (Tanaemyrmex) punctulatus termitarius* Emery. This subspecies of a widely distributed and very variable Neotropical ant is of peculiar interest because its behavior is the basis of one of Wasmann's ingenious but apocryphal hypotheses. It was found by Heyer and Silvestri in the mounds of several species of termites (see Appendix B, p. 232) in Southern Brazil. Heyer believed that the relations of the *Camponotus* to the termites are "völlig friedliche," to use Wasmann's expression, because there was no struggle between them when the termitary was broken open. The ants were seen on several occasions, however, to carry off the termites, but this behavior, so like that of *C. novogranadensis*, was interpreted by Heyer (probably "mit Unrecht," as Wasmann remarks) as due to the excited ants mistaking the termites for their own brood when the interior of their nest was suddenly illuminated. According to Wasmann (1915), Heyer wrote him on April 10, 1895 as follows "in regard to the explanation of the symbiosis between that black *Camponotus* and the termites: "According to my previous observations the mounds of the large termites (*Cornitermes cumulans* Koll. and *similis* Hag.) always consist of clay, those of the medium-sized species (*Eutermes fulviceps* Silv.) partly of clay and partly of ordinary earth, those of the small species (*Anoplotermes ater* and *morio*) always of earth. These earthen mounds (of *Eutermes* and *Anoplotermes*), which are not very strong or compact, seem to be specially preferred by the black ants, and to such a degree that one rarely finds one of these earthen mounds on or in which they have not established themselves. Now although the termites are compelled to let part of their dwelling to these intruders, they seem not only to yield to the stronger but must also derive some benefit from their neighbors. I infer this from the following observa-

tion: I found a nest of these black ants, consisting of loose earth, above which in a layer of more compact earth small termites (*Anoplotermes morio* Latr.) had established themselves. Here obviously, the termites and ants had exchanged roles, and the former had sought out the latter." Wasmann then proceeds: "H. v. Ihering found at Pedras brancas (near Porto Alegre) a fecundated queen of *Camponotus termitarius* in an earthen termite structure. It seems to be rather



FIGURE 8. Small fungiform termitary of *Cubitermes* sp. inhabited by *Camponotus* (*Myrmotrema*) *perrisi jucundus* Santschi, from Garamba, Belgian Congo. The numerous entrances of the ants are clearly seen, especially at the base. (Photograph by H. O. Lang.)

certain from Heyer's observation and this last datum that after their nuptial flight the fecundated queens of that black *Camponotus* seek out the earthen mounds of termites (*Eutermes* and *Anoplotermes*) for the purpose of establishing their colonies in them. The ants derive from the symbiosis with the termites the advantage of securing a comfortable dwelling which suits their nidamental instincts and relieves them from the labor of building their own earthen mounds. But what advantage do the termites secure from the association? Probably protection from other carnivorous species of ants that are

fond of attacking termite nests in order to carry off the soft-skinned termites as prey. If on such an occasion they chance on a nest inhabited by the black *Camponotus*, they are compelled to fight with a well-armed adversary, which energetically protects the outer layer of the nest from enemies and prevents their penetration into the portion inhabited by the termites. Hence these termite ants may be regarded as a kind of protective phalanx for the termite colonies, and their relations to the latter would thus have the character of a protective symbiosis, more efficient than that obtaining between the myrmecophilous plants and their ant protectors. For this relation of *Camponotus termitarius* to its hosts, we may therefore introduce the beautiful Greek term "*phylacobiosis*." "

Silvestri (1902, 1903), who observed *C. termitarius* in Matto Grosso, gives us a very different and much less romantic account of its relations to the termites. He says: "This ant lives in open, damp fields and constructs nests on the ground 50 to 70 centimeters high. In such a nest one often finds *Anoplotermes cingulatus* and *tenebrosus* but their presence in this situation may be regarded as quite accidental. At other times nests of *Eutermes arenarius fulviceps* are found applied to one side of the *Camponotus* nests and this, too, is quite accidental. Both the *Camponotus* and the above mentioned species of termites usually live far from each other."¹

I have quoted Wasmann at length because his phylacobiosis hypothesis is such a fine example of arm-chair speculation. As a matter of fact, no conscientious student of ants and termites in the tropics has been able to observe any such behavior, first, because as Escherich (1911) remarks, not infrequently colonies of several species of ants are found to occupy galleries in the same termitary, and second, because the connotations of "the beautiful Greek term phylacobiosis" are too anthropomorphic. Before assuming that the *C. termitarius* colony actually functions as a guard we should know the enemies from which it protects the termites and its behavior towards the latter should be non-aggressive. Many ants, of course, will defend their own nest from enemies and if it happens to occupy a portion of a termitary they may be incidentally defending the termitary at the same time but not the termites. This is clearly seen in such cases as *Iridomyrmex sanguineus*. Moreover, *C. termitarius* is,

¹ Wasmann (1915 p. 363 *nota*) believed that the form cited as *C. termitarius* by Silvestri was really *C. (Myrmobrachys) fastigiatus* Roger, which "in the same regions builds high, independent, earthen nests," but it is more probable that he saw the nests of both species and failed to distinguish them.

in all probability, no more aggressive than other small species of *Camponotus*, of which *C. novograndensis* is a typical example, and would not be able to defend a termitary against the attacks of such a small but persistent raider as *Termitopone marginata*, the only ant enemy of these insects known to inhabit the same geographical area. I therefore agree with Maidl (1933) when he says that "in most instances we may assume that the termites tolerate the presence of alien ants, (Meliponid) bees, and other termites, which usurp portions of their nest, simply because they can do nothing else and also because they do not, like many ants, possess the lust of aggression and strategy of attack that might enable them to expell the intruders."

5. TERMITOXENY

Owing to the considerable differences in trophic and reproductive behavior between ants and termites we should hardly expect these insects to live in mixed colonies. Nevertheless, there are two cases in the literature, which have been supposed to exhibit more intimate symbiotic relations than those considered in the preceding section. One of these cases is *Crematogaster* (*Orthocrema*) *victima alegrensis* Forel, found by Heyer only in termitaries of *Eutermes* (= *Nasutitermes*) *fulviceps* Silvestri near Porto Alegre and São Leopoldo, Brazil and brought to the attention of myrmecologists by Wasmann (1901-02, 1915). This investigator was informed by Heyer that the *Crematogaster* nest "was in the middle of the termite nest and surrounded by the dense clay layer of the termite construction. The galleries, characteristic of the termites, had not been altered by the ants. The ants were quite as phlegmatic as the termites; when I destroyed the nest, no excitement was observed." These meager notes, after alembication in Wasmann's fancy, yielded the following interpretation: "Even the position of this ant nest in the middle of the termite nest is very striking for a *Crematogaster*, since most species of this genus build carton nests. Since, moreover, the *Crematogaster*, unlike the other species of the genus, which are very pugnacious and make great use of their painful stings, did not on this occasion attack the termites as the probable disturbers of their peace, it is very probable that the symbiosis between the species of *Crematogaster* and the *Eutermes* is of a *peaceable* nature, and not of an *inimical* nature as in the thief-ants of the genus *Solenopsis*. What the relations are that unite *Crematogaster alegrensis* with *Eutermes fulviceps* is still unknown and it would be premature to introduce a new Greek name, as one is now so fond of

doing in similar cases.¹ Perhaps we are here concerned with a regular (gesetzmässigen) case of Forel's "parabiosis."

To one familiar with *Crematogaster* species in the field, Wasmann's account seems almost grotesque. It is well known that carton nests are constructed by comparatively few even among the arboreal species of this huge genus and that numerous forms, especially of the subgenus *Orthocrema*, form rather small colonies which nest in the soil, are very peaceable or phlegmatic and make little use of their feeble stings. Furthermore, *C. alegrensis* cannot be regarded as parabiotic because its nesting habits are entirely different from those of the parabiotic ants described by Forel, Mann and myself. It is either a lestiobiotic or more probably an inquiline ant and is therefore included in my Appendix B.

The second case is the Indomalayan *Liomyrmex aurianus* Emery, on which I published a note in 1914. Professor C. F. Baker found the minute, yellow, blind workers of this ant "abundant with termites—living in the same chambers with these in entire amity." The termites which accompanied the ants proved to be workers and soldiers of *Macrotermes gilvus* Hagen. At the time I was inclined to regard *aurianus* as termitoxenic but Baker's "entire amity" now seems to me to admit of a different interpretation. The taxonomic affinities of the insect suggest that it may be termitolestic and that the workers when present in the termite chambers, like the thief-ants (*Solenopsis*, *Carebara*, etc.), are overlooked by their much larger hosts. That *aurianus* is not a termitoxenic ant is indicated also by the fact that von Buttel-Reepen (Forel 1913) found it nesting independently of termites in a large tree-trunk at Selangor, Malacca. The females of *Liomyrmex*, which measure 10.2 mm. and are therefore much larger than the workers (3–3.3 mm.), are so peculiar in the structure of their petiole and postpetiole that on two occasions very competent myrmecologists have described them as the types of distinct genera (*Laparo-myrmex* Emery and *Promyrma* Forel).

Up to the present time, therefore, no clear cases of friendly relations between ants and termites have been recorded. There is, however, one unpublished but rather fragmentary observation of my own, which, I believe, suggests the existence of such relations. On September 18, 1931, near Mullewa, West Australia, I came upon a colony of diminutive termites nesting under a flat stone in earthen galleries which they had built in a bunch of dry grass. On breaking

¹ As for example, when Wasmann himself introduces "the beautiful Greek term phylacobiosis" (see p. 212 *supra*).

open one of the galleries I saw several small ants of the same size and color as the somewhat more numerous termites and moving about among them. After carefully collecting the occupants of the gallery and making allowance for escaping individuals, the ant-colony was found to comprise only 25 to 30 workers and a single ergatomorphic female (queen). I failed to find any additional ants in the termitary and saw no traces of their brood. The female and more than half of the workers attracted my attention because their gasters were enormously distended (Fig. 9). This distension (physogastry) was not due to liquid stored in their crops but to an unusual accumulation of fat. The termites have been identified by Dr. Emerson as *Nasutitermes* (*Tumulitermes*) *peracutus* Hill. He informs me that "this species was described in 1915 from Beverley, York, Chidlow's Wells and Merredin, West Australia. According to Hill "Mr. Clark states that this species does not build mounds but tunnels in the soil under large stones. It is a grass-cutting species." " The ants belong to an undescribed species of *Stigmacros*, an exclusively Australian genus of which eleven species are described and of which Mr. John Clark and I have taken quite a number of unpublished forms. Although I have examined hundreds of *Stigmacros* from numerous localities in Eastern, Southern and Western Australia, I have seen no traces of physogastry except in the Mullewa specimens. Since the ants were living in what appeared to be friendly relations with their hosts, I suspect that they are fed by the termite workers and that the physogastry of the female and so many of the workers, like the physogastry of the termite workers and queens, is a result of this feeding. At any rate, there is here a very interesting problem for some resident West Australian entomologist. I append a description with figures of the ant.

***Stigmacros termitoxenus* sp. nov.**

Worker (Fig. 9 a-e). Length 2.7-3.4 mm.

Head subtrapezoidal, slightly longer than wide, distinctly narrower in front than behind, with feebly convex sides, broadly rounded posterior corners and straight posterior border. Eyes rather large and convex, somewhat longer than one fourth of the sides of the head, situated just behind its median transverse diameter. Mandibles narrow, convex, 4-toothed, the apical tooth long. Clypeus convex, sharply carinate, with entire, broadly rounded and projecting anterior border. Frontal area subtriangular, broader than long, indistinctly delimited posteriorly. Frontal carinae straight, slightly diverging behind; frontal groove absent. Antennae long and slender; scapes

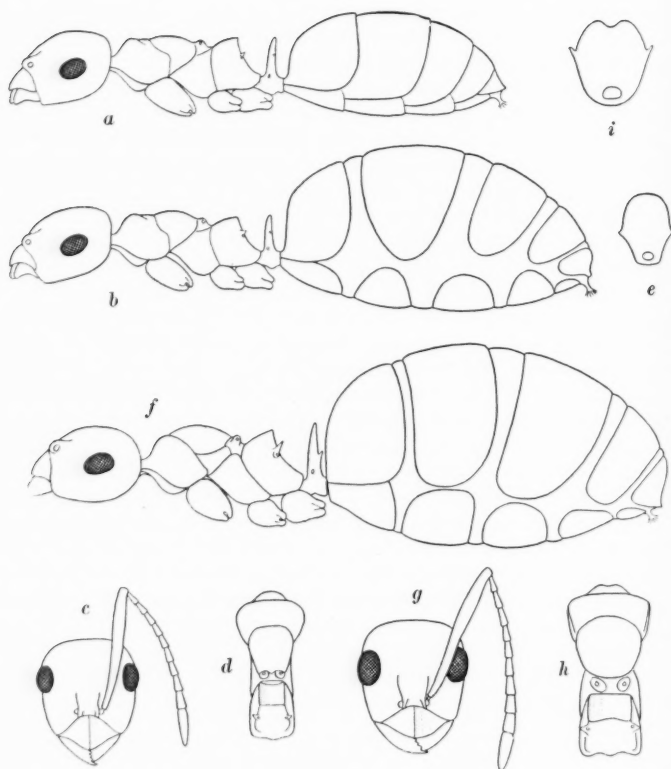


FIGURE 9. *Stigmatocros termitoxenus* sp. nov. *a*, normal worker, in profile; *b*, physogastric worker; *c*, head of worker, dorsal aspect; *d*, thorax of same, dorsal aspect; *e*, petiole, posterior aspect; *f*, physogastric, ergatomorphic female, in profile; *g*, head of same; *h*, thorax, dorsal aspect; *i*, petiole, posterior aspect.

extending slightly more than two-fifths of their length beyond the posterior border of the head; funiculi not conspicuously enlarged at their tips and with all their joints decidedly longer than broad, the second joint one and one-half times, joints 3-9 twice as long as broad, the terminal joint slightly shorter than the ninth and tenth together.

Thorax rather narrow; pronotum, without the neck, distinctly broader than long, with rounded, not very prominent humeri and medially somewhat impressed dorsal surface, in profile with sloping anterior and horizontal posterior surface; promesonotal suture distinct and impressed; mesonotum subtrapezoidal, one fourth longer than broad, with straight, posteriorly converging sides, in profile evenly convex above and slightly higher than the pronotum; mesometanotal suture obsolete, replaced by a distinct transverse impression; metanotum distinct, twice as broad as long, in profile convex anteriorly on each side, sloping posteriorly to the pronounced metaepinotal constriction, the stigmata not very prominent; epinotum distinctly longer than wide, subcuboidal, the base in profile half as long as the evenly and feebly concave, rather steeply sloping declivity, straight and sloping upward and backward from the metaepinotal constriction, its dorsal surface seen from above rectangular, concave in the middle, its sides marginate and distinctly angulate posteriorly, the stigma-bearing tooth on each side of the declivity small and acute, not longer than wide at its base. Petiolar scale in profile thin, as high as the epinotum, with flattened posterior, distinctly convex anterior surface and sharp apex; seen from behind with rounded sides, which are only broadly and feebly dentate below, narrowed above, with straight, transverse or very feebly concave superior border. Gaster of the usual elliptical shape, in the physogastric specimens with the sclerites widely separated and the intersegmental membranes exposed. Legs rather long.

Shining, reticulate, the thorax and the posterior portion of the head more coarsely so that these regions are more subopaque. Mandibles smooth and shining, sparsely and not very coarsely punctate.

Pilosity whitish, very sparse, short and blunt, present only on the gaster, head, clypeus, mandibles and tips of scapes; pubescence white, appressed, absent on the body, moderately dense on the antennae, very dilute on the legs.

Castaneous; posterior portion of head and in some specimens also the gaster darker and more blackish; mandibles, antennae, legs and petiole pale yellowish brown or brownish yellow; mandibular teeth black.

Female (apterous and ergatomorphic) (Fig. 9 f-h). Length 4.6 mm. Closely resembling the worker, but the head is broader, as broad as long, with somewhat less convex sides, slightly larger eyes but without ocelli. Thorax stouter, its pronotum broader in proportion to its length and with more prominent humeri; mesonotum as broad as long and more convex than in the worker. Petiole slightly higher than

epinotum and even thinner than in the worker, with the apical border narrower and distinctly emarginate in the middle. Gaster very large, physogastric, decidedly longer than the head and thorax together.

Sculpture, pilosity and color as in the worker except that the legs are paler yellow and the gaster is brown like the thorax.

Described from ten workers and a single female taken at Mullewa, West Australia in a small termitary of *Nasutitermes* (*Tumulitermes*) *peracutus* Hill.

This species is most closely related to *S. occidentalis* Crawley, the only other described species from West Australia, but differs in its somewhat larger size, decidedly larger eyes, much longer scapes and funicular joints, less pronounced humeri, longer mesonotum, smaller stigma-bearing epinotal teeth and broader and laterally more convex petiolar scale.

APPENDIX A

A LIST OF TERMITOLESTIC ANTS

- Monomorium termitobium* Forel. With *Microcerotermes sikorae* (Wasmann) (Sikora)—Madagascar (Wasmann 1902).
- Anillomyrma decamera* Emery. As thief-ant in fungus gardens of *Odontotermes* (*Cycлотermes*) *redemanni* (Wasmann) (W. Horn)—Ceylon (Wasmann 1902); in termitary of *Macrotermes gilvus* (Hagen) (N. A. Kemner)—Java.
- Liomyrmex aurianus* Emery. In galleries with *Macrotermes gilvus* Hagen (C. F. Baker)—Philippines (Wheeler 1914).
- Tranopelta heyeri* Forel. In termitaries of *Nasutitermes fulviceps* (Silvestri) and *Anoplotermes meridianus* Emerson (C. Heyer)—Southern Brazil (Wasmann 1902, 1915).
- Solenopsis* (*Diplorhoptrum*) *azteca* Forel. In peripheral cells of a termitary of *Amitermes medius* Banks (A. E. Emerson)—Panama.
- Solenopsis* (*Diplorhoptrum*) *brevicornis* Emery. In termitary of *Anoplotermes ater* Hagen (J. P. Schmalz)—Southern Brazil (Wasmann 1902, 1915).
- Solenopsis* (*Diplorhoptrum*) *clarki* Crawley. In termitary (L. Glauert)—West Australia.
- Solenopsis* (*Diplorhoptrum*) *hammari* Mayr. From cells of *Nasutitermes beebei* Emerson in a bracket-fungus (A. E. Emerson)—British Guiana.
- Solenopsis* (*Diplorhoptrum*) *hermione* Wheeler. With termites (I. Molino)—Panama.
- Solenopsis* (*Diplorhoptrum*) *lacviceps* Mayr. In a termitary of *Nasutitermes* (*Constrictotermes*) *caviceps* (Holmgren) and another termitary deserted by this termite but occupied by *N. costalis* (Holmgren) (A. E. Emerson)—British Guiana.
- Solenopsis* (*Diplorhoptrum*) *molesta* (Say). With *Reticulitermes flavipes* (Kollar), *R. virginicus* Banks and *R. lucifugus* (Rossi) (King, Hayes, Forel, Wheeler, etc.)—Eastern and Middle United States.
- Solenopsis* (*Diplorhoptrum*) *schmalzi* Forel. In termitary of *Anoplotermes ater* (Hagen) (J. P. Schmalz)—Southern Brazil (Forel 1894, Wasmann 1902, 1915).
- Solenopsis* (*Diplorhoptrum*) *schmalzi* var. *flavcolens* Forel. In termitary of *Anoplotermes ater* (Hagen) (J. P. Schmalz)—Southern Brazil (Forel 1894, Wasmann 1902, 1915).
- Solenopsis* (*Diplorhoptrum*) *tenuis* Mayr. With *Termes* (*T.*) sp. in log (A. E. Emerson)—Panama.

- Solenopsis (Diplophoptrum) texana carolinensis* Forel. With termites (A. Forel)—North Carolina (Forel 1901).
- Solenopsis (Diplophoptrum) texana truncorum* Forel. With termites (A. Forel)—North Carolina (Forel 1901).
- Lophomyrmex quadrispinosus* (Jerdon). In mound termitary of *Odontotermes (Cycloptermes) redemanni* (Wasmann) (W. Horn)—Ceylon (Wasmann 1902); in termitary of *Odontotermes javanicus* Holmgren (N. A. Kemner)—Java.
- Lophomyrmex quadrispinosus* var. *opaciceps* Viehmeyer. In termitaries of *Termes* sp. and *Odontotermes grandiceps* Holmgren (N. A. Kemner)—Java.
- Trigonogaster recurispinosa kemneri* subsp. nov. In termitary of *Termes* sp. (N. A. Kemner)—Java.
- Analeus (Lecanomyrma) butteli* Forel. In small walnut-sized cavities in mantle of termitaries of *Odontotermes (Cycloptermes) redemanni* (Wasmann) and *O. (Hypotermes) obscuriceps* (Wasmann) (H. v. Buttel-Reepen)—Ceylon (Forel 1913).
- Oligomyrmex jacobsoni* Forel. In termitaries of *Termes* sp. (N. A. Kemner)—Java.
- Oligomyrmex taprobanæ* Forel. Nesting usually in mantle portions of termitaries of *Odontotermes (Hypotermes) obscuriceps* (Wasmann) (K. Escherich)—Ceylon (Forel 1911, Escherich 1911).
- Æromyrma nosindambo* Forel. With *Microcerotermes sikoræ* (Wasmann) and *Capritermes capricornis* Wasmann (Sikora)—Madagascar (Wasmann 1902).
- Æromyrma petulca* Wheeler. In a small fungiform termitary probably made by *Cubitermes fungifaber* (Sjöstedt) (Lang and Chapin)—Belgian Congo (Wheeler 1922).
- Æromyrma sundaica* Forel. In a moist earthen termitary of *Nasutitermes nasutus* (Holmgren) (H. v. Buttel-Reepen)—Sumatra (Forel 1913); in a termitary of *Odontotermes javanicus* Holmgren (N. A. Kemner)—Java.
- Erebomyrma longi* Wheeler. Very probably with subterranean termites (W. H. Long)—Texas (Wheeler 1903).
- Paedalgus escherichi* Forel. In small geode-like chambers in mantle portion of termitaries of *Odontotermes (Hypotermes) obscuriceps* Wasmann (K. Escherich)—Ceylon (Forel 1911, Escherich 1911).
- Paedalgus infimus* Santschi. Very probably with termites—French Guinea.
- Paedalgus termitolestes* Wheeler. In mound termitary near fungus-gardens of *Acanthotermes militaris* Hagen (Lang and Chapin)—Belgian Congo (Wheeler 1922, Emerson 1928).

- Carebara junodi* Forel. Inhabiting mound termitaries of *Acanthotermes* (*Pseudacanthotermes*) *spiniger* Sjöstedt (J. Bequaert)—Belgian Congo (Bequaert 1913).
- Carebara lignata* Westwood. In termitaries of *Odontotermes javanicus* Holmgren (N. A. Kemner)—Java.
- Carebara osborni* Wheeler. In a mound termitary of *Macrotermes natalensis* Haviland (Lang and Chapin)—Belgian Congo (Wheeler 1922).
- Carebara vidua* F. Smith. In mound termitaries of *Macrotermes natalensis* Haviland (G. D. Haviland)—Natal (Forel 1901, Wasmann 1902).
- Carebara winifredae* Wheeler. In a large subterranean termitary of *Syntermes snyderi* Emerson (A. E. Emerson)—British Guiana (Wheeler 1922).

APPENDIX B

A LIST OF INQUILINE ANTS FROM TERMITARIES

Dorylinae

Dorylus (Dichthadia) laevigatus F. Smith. In an abandoned mound termitary (H. v. Buttel-Reepen)—Ceylon (Forel 1913).

Dorylus (Rhognus) termitarius Wasmann. In lower portion of a termitary of *Acanthotermes (Pseudacanthotermes) spiniger* Sjöstedt (H. Kohl)—Belgian Congo (Wasmann 1911).

Leptanillinae

Leptanilla butteli Forel. In an earthy carton termitary of *Capritermes nemorosus* (Haviland) (H. v. Buttel-Reepen)—Malacca (Forel 1913).

Cerapachyinae

Phyracaces langi Wheeler. In a fungiform termitary of *Cubitermes* sp. (Lang and Chapin)—Belgian Congo (Wheeler 1922).

Cylindromyrmex brasiliensis Emery. In the galleries of termites (*Calotermes* ?) (Hetschko)—Brazil (Mayr 1887).

Cylindromyrmex williamsi Wheeler. In galleries of *Calotermes pacificus* Banks in dead branches of *Maytenus obovata* Hooker (W. M. Wheeler)—Galapagos Islands (Wheeler 1924).

Ponerinae

Stigmatomma (Fulakora) minuta Forel. In an earthy carton termitary containing two species of termites, *Amitermes dentatus* (Haviland) and *A. minor* Holmgren (H. v. Buttel-Reepen)—Eastern Sumatra (Forel 1913).

Prionopelta kraepelini Forel. In a termitary of *Odontotermes javanicus* Holmgren (N. A. Kemner)—Java.

Holcoponera brasiliensis Emery. With *Anoplotermes ater* (Hagen) (J. P. Schmalz)—Southern Brazil (Wasmann 1915).

Centromyrmex feae (Emery). In fungus gardens of *Microtermes pallidus* (Haviland) (H. v. Buttel-Reepen)—Malacca (Forel 1913); with *Termes* sp., *Odontotermes javanicus* Holmgren, *Capritermes* sp. and *Nasutitermes* sp. (N. A. Kemner)—Java.

Centromyrmex feae var. *ceylonicus* Forel. "Always with termites" (K. Escherich)—Ceylon (Forel 1911); in termitaries of *Heterotermes ceylonicus* Holmgren (H. v. Buttel-Reepen)—Ceylon (Forel 1913).

Odontoponera transversa F. Smith. In galleries of *Termes* sp. (N. A. Kemner)—Java.

- Ophthalmopone berthoudi* Forel. In deserted mound termitaries (G. Arnold)—Rhodesia (Arnold 1915).
- Bothroponera rufipes* (Jerdon). In a termitary of *Capritermes* sp. (N. A. Kemner)—Java.
- Euponera* (*Brachyponera*) *lutea* (Mayr). In basal galleries of termitaries of *Amitermes wilsoni* Hill (W. M. Wheeler)—Queensland (Wheeler 1918); in termitaries (L. Glauert)—West Australia.
- Euponera* (*Brachyponera*) *luteipes* (Mayr). In a termitary of *Schedorhinotermes javanicus* Kemner (N. A. Kemner)—Java.
- Euponera* (*Mesoponera*) *melanaria* Emery. In abandoned termitaries (H. v. Buttet-Reepen)—Ceylon (Forel 1913).
- Euponera* (*Mesoponera*) *rubra* F. Smith var. *javana* Forel. In a termitary of *Schedorhinotermes javanicus* Kemner (N. A. Kemner)—Java.
- Pseudoponera amblyops* Emery. In a termitary of *Odontotermes javanicus* Holmgren (N. A. Kemner)—Java.
- Pseudoponera butteli* Forel. Under leaves and in fungus gardens of *Termes* sp. (H. v. Buttet-Reepen)—Java (Forel 1913).
- Cryptopone testacea* (Motschulsky). From an earthy carton termitary of *Capritermes nemorosus* Haviland (H. v. Buttet-Reepen)—Malacca (Forel 1913).
- Emeryopone buttel-reepeni* Forel. In an earthy carton termitary of *Amitermes dentatus* (Haviland) and *A. minor* Holmgren. (H. v. Buttet-Reepen)—Eastern Sumatra (Forel 1913).
- Ponera abeillei assmuthi* Forel. In a termitary of *Coptotermes travians* (Haviland) (J. Assmuth)—India (Wasmann 1915).
- Ponera butteli* Forel. In an earthy carton termitary of *Amitermes minor* Holmgren (H. v. Buttet-Reepen)—Sumatra (Forel 1913).
- Ponera confinis* Roger. In a termitary of *Capritermes incola* (Wasmann) (H. v. Buttet-Reepen)—Ceylon (Forel 1913).
- Ponera confinis* var. *aikeni* Forel. In a fungus chamber of *Odontotermes ceylonicus* (Wasmann) (H. v. Buttet-Reepen)—Ceylon (Forel 1913).
- Ponera confinis wroughtoni* Forel. In a termitary of *Heterotermes indicola* (Wasmann) (J. Assmuth)—India (Wasmann 1915).
- Ponera lumpurensis* Forel. In an earthy carton termitary of *Capritermes nemorosus* Haviland (H. v. Buttet-Reepen)—Malacca (Forel 1913).
- Ponera pygmaea* Forel. In an earthy carton termitary of *Capritermes semarangi* Holmgren (H. v. Buttet-Reepen)—Sumatra (Forel 1913).

- Ponera schmalzi* Emery. With *Nasutitermes fulviceps* (Silvestri) (J. P. Schmalz)—Southern Brazil (Wasmann 1915).
- Ponera trigona* Mayr. With *Anoplotermes ater* (Hagen) (J. P. Schmalz)—Southern Brazil (Wasmann 1915).
- Leptogenys (Lobopelta) diminuta* F. Smith. In mantle of clay mound termitary of *Odontotermes (Cycloptermes) obesus* Rambur (J. Assmuth)—India (Wasmann 1915).
- Leptogenys (Lobopelta) myops* Emery. In termitary of *Nasutitermes* sp. (N. A. Kemner)—Java.
- Leptogenys (Lobopelta) peuqueti* Ern. André. In termitary of *Termes* sp. ? (N. A. Kemner)—Java.
- Anochetus altisquamis* Mayr. In termitary of *Anoplotermes ater* (Hagen) (Schmalz)—Southern Brazil (Wasmann 1915).
- Anochetus gracfei* Mayr. In termitary of *Capritermes* sp. (N. A. Kemner)—Java.
- Anochetus jacobsoni* Forel var. *taipingensis* Forel. In a termitary of *Homalotermes foraminifer* (Haviland) (H. v. Buttet-Reepen)—Malacca (Forel 1913).
- Anochetus longifossatus butteli* Forel. In a termitary of *Heterotermes ceylonicus* Holmgren (H. v. Buttet-Reepen)—Ceylon (Forel 1913).
- Odontomachus haematoda* L. Frequently nesting in "chimneys" of mound termitaries (K. Escherich)—Ceylon (Forel 1911); in a termitary of *Microcerotermes* sp. (N. A. Kemner)—Java.
- Odontomachus rixosus* F. Smith var. *conifer* Forel. With *Macrotermes gilvus* (Hagen) in decayed wood (H. v. Buttet-Reepen)—Java (Forel 1913).

Myrmicinae

- Metapone greeni* Forel. In galleries of a decayed branch infested with two species of termites (Calotermes?) (E. Green)—Ceylon (Forel 1911).
- Pogonomyrmex (Ephedomyrmex) naegeli* Forel. In a termitary of *Nasutitermes fulviceps* (Silvestri) (C. Heyer)—Southern Brazil (Wasmann 1902).
- Pheidole aglaë* Forel. In decayed wood traversed by populous galleries of *Microtermes pallidus* (Haviland). (H. v. Buttet-Reepen)—Java (Forel 1913).
- Pheidole attila* Forel. In mantles of mound termitaries of *Macrotermes gilvus* (Hagen) (H. v. Buttet-Reepen)—Sumatra (Forel 1913).
- Pheidole butteli* Forel. In a bulbous, earthy carton termitary of *Capritermes minor* Holmgren (H. v. Buttet-Reepen)—Sumatra (Forel 1913).

- Pheidole capellinii* Emery. In a termitary of *Odontotermes ceylonicus* Holmgren (N. A. Kemner)—Java.
- Pheidole caffra senilifrons* Wheeler. In a small fungiform termitary of *Cubitermes* sp. (Lang and Chapin)—Belgian Congo (Wheeler 1922).
- Pheidole megacephala impressifrons* Wasmann. In an abandoned termitary of *Cubitermes pallidiceps* (Sjöstedt) (J. Bequaert)—Belgian Congo (Bequaert 1913).
- Pheidole megacephala punctulata* Mayr. In fungiform termitaries of *Cubitermes* sp. in swamps. (Lang and Chapin)—Congo (Wheeler 1922); in external galleries of an inhabited termitary (J. Bequaert)—Belgian Congo (Bequaert 1925).
- Pheidole nodgii* Forel. In a termitary of *Schedorhinotermes javanicus* Kemner (N. A. Kemner)—Java.
- Pheidole rodoszowskii* Mayr. In termitaries of *Nasutitermes fulviceps* (Silvestri) (C. Heyer)—Southern Brazil (Wasmann 1902); in log with termites (Miss L. Hare)—Panama.
- Pheidole schoutedeni* Forel. In an abandoned termitary of *Cubitermes pallidiceps* (Sjöstedt) (J. Bequaert)—Belgian Congo (Bequaert 1913).
- Pheidole tandjongensis* Forel. Under bark with *Odontotermes butteli* Holmgren (H. v. Buttel-Reepen)—Sumatra (Forel 1913).
- Pheidole termitobia* Forel. With *Anoplotermes ater* Hagen and *A. meridianus* Emerson (C. Heyer)—Southern Brazil (Wasmann 1902, 1915).
- Crematogaster (Orthocrema) baduvi* Forel. With *Termes* sp? and in a fragment of a carton termitary of an unidentified termite on tree (N. A. Kemner)—Java.
- Crematogaster (Orthocrema) biroi* Mayr var. *aitkeni* Forel. With *Odontotermes (Hypotermes) obscuriceps* (Wasmann) (K. Escherich)—Ceylon (Forel 1911).
- Crematogaster (Orthocrema) limata* F. Smith. In a termitary of *Nasutitermes (Constrictotermes) cavifrons* (Holmgren) (A. E. Emerson)—British Guiana.
- Crematogaster (Orthocrema) quadriformis*. With *Nasutitermes fulviceps* (Silvestri) (C. Heyer)—Southern Brazil (Forel 1901, Wasmann 1915).
- Crematogaster (Orthocrema) rectinota* Forel. Under stones, "very often in close proximity to the nests of termites" (G. Arnold)—Rhodesia (Arnold).
- Crematogaster (Orthocrema) victima aleggensis* Forel. With *Nasutiter-*

- mes fulviceps* (Silvestri) (Schupp and Heyer)—Southern Brazil (Forel 1894, Wasmann 1902, 1915).
- Crematogaster (Acrocoelia) artifex* Mayr. With *Nasutitermes matangensis* (Haviland) (H. v. Buttel-Reepen)—Sumatra (Forel 1913); in mantle of a termitary of *Termes* sp. (N. A. Kemner)—Java.
- Crematogaster (Acrocoelia) castanea rufonigra* Emery var. *mediorufa* Forel. In superficial galleries of a small, inhabited, dome-shaped termitary (J. Bequaert)—Belgian Congo (Bequaert 1925).
- Crematogaster (Acrocoelia) impressa* Emery var. *sapora* Forel. In cavities of small fungiform termitaries of *Cubitermes* sp. (Lang and Chapin)—Belgian Congo (Wheeler 1922).
- Crematogaster (Acrocoelia) rothneyi* Mayr. Under bark with *Nasutitermes (Trinervitermes) biformis* (Wasmann); also with *Capritermes incola* (Wasmann) and in mound termitaries of *Odontotermes (Cyclotermes) redemanni* (Wasmann) (W. Horn)—Ceylon (Wasmann 1902).
- Crematogaster (Acrocoelia) schultzei* Forel. In a termitary of *Amitermes runconifer* Silvestri (L. Schultze)—Little Namaland (Forel 1910).
- Crematogaster (Sphaerocrema) bequaerti* Forel. Repeatedly in abandoned dome-shaped termitaries (J. Bequaert)—Belgian Congo (Bequaert 1913).
- Crematogaster (Paracrema) spengeli taipingensis* Forel. In an arboreal carton termitary of *Nasutitermes matangensis* Haviland (H. v. Buttel-Reepen)—Sumatra (Forel 1913).
- Vollenhovia oblonga rufescens* Emery var. *reepeni* Forel. Under bark and in termitaries (H. v. Buttel-Reepen)—Malacca (Forel 1913).
- Vollenhovia opacinoda* Forel. In a woody carton termitary of *Nasutitermes matangensis* Haviland (H. v. Buttel-Reepen)—Sumatra (Forel 1913).
- Monomorium (Monomorium) angustinode* Forel. In galleries of dome-shaped termitaries of *Cubitermes pallidiceps* (Sjöstedt) (J. Bequaert)—Belgian Congo (Bequaert 1913).
- Monomorium (Monomorium) butteli* Forel. In a woody carton termitary of *Labritermes buttel-reepeni* Holmgren (H. v. Buttel-Reepen)—Sumatra (Forel 1913).
- Monomorium (Monomorium) floricola* (Jerdon) var. *furinum* Forel. In a ligneous termitary of *Coptotermes* sp. (K. Escherich)—Ceylon (Forel 1911).
- Monomorium (Monomorium) pharaonis* (Linn.) With *Nasutitermes (Trinervitermes) biformis* (Wasmann) (J. Assmuth)—India (Wasmann 1915).

- Monomorium* (*Monomorium*) *prossae* Forel. Almost invariably associated with termites (A. M. McGregor)—Rhodesia (Arnold 1915).
- Monomorium* (*Monomorium*) *sordidum* Forel var. *nigriventre* Forel. In a termitary (L. Glauert)—West Australia.
- Monomorium* (*Xeromyrmex*) *salomonis delagoënsae* Forel. With *Amitermes unidentatus* Wasmann (H. Brauns)—Cape Province (Wasmann 1902).
- Monomorium* (*Xeromyrmex*) *salomonis termitarium* Forel. Occupying part of a termitary (L. Schultze)—Kalahari Desert, Bechuanaland (Forel 1910).
- Monomorium* (*Parholcomymex*) *destructor* (Jerdon). In mound termitaries of *Odontotermes* (*Cylotermes*) *redemanni* (Wasmann) and *O.* (*Hypotermes*) *obscuriceps* (Wasmann) (K. Escherich)—Ceylon (Forel 1911); in a termitary of *Coptotermes travians* (Haviland) (J. Assmuth)—India (Wasmann 1915); in a termitary of *Termes* sp. ? (N. A. Kemner)—Java.
- Monomorium* (*Parholcomymex*) *destructor kalahariense* Forel. In a termitary of *Amitermes runconifer* Silvestri (L. Schultze)—Kalahari Desert, Bechuanaland (Forel 1910).
- Monomorium* (*Parholcomymex*) *destructor kalahariense* var. *despectum* Forel. In an abandoned dome-shaped termitary of *Cubitermes sankuruensis* Wasmann (J. Bequaert)—Belgian Congo (Bequaert 1913).
- Monomorium* (*Parholcomymex*) *destructor mayri* Forel. In fungus gardens of *Macrotermes gilvus* (Hagen) (H. v. Buttel-Reepen)—Sumatra (Forel 1913).
- Monomorium* (*Parholcomymex*) *epinotale* Santschi. In a termitary (P. Callewaert)—Belgian Congo (Santschi 1923).
- Monomorium* (*Parholcomymex*) *gracillimum robustius* Forel. In small fungiform termitaries of *Cubitermes* sp. (Lang and Chapin)—Belgian Congo (Wheeler 1922).
- Monomorium* (*Lampromymex*) *bequaerti* Forel. In galleries of a dome-shaped termitary of *Cubitermes tenuiceps* (Sjöstedt) (J. Bequaert)—Belgian Congo (Bequaert 1913).
- Monomorium* (*Lampromymex*) *ilia* Forel. In a termitary (L. Glauert)—West Australia.
- Solenopsis* (*Solenopsis*) *geminata* (Fabricius). "Found repeatedly in termitaries" (A. Schupp and C. Heyer)—Southern Brazil (Wasmann 1902); in termitaries of *Anoplotermes cingulatus* (Burmeister) and *A. tenebrosus* (Hagen) (F. Silvestri)—Argentina (Silvestri 1902, 1903).

- Solenopsis (Solenopsis) puncticeps caffra* Emery. With *Angulitermes frontalis* (Silvestri) (L. Schultze)—Kalahari Desert, Bechuanaland (Forel 1910); in an abandoned dome-shaped termitary (J. Bequaert)—Belgian Congo (Bequaert 1913).
- Meranoplus bicolor lucidus* Forel. In a termitary of *Capritermes* sp. (N. A. Kemner)—Java.
- Tetramorium bequaerti* Forel. In a dome-shaped termitary of *Cubitermes tenuiceps* (Sjöstedt) (J. Bequaert)—Belgian Congo (Bequaert 1913).
- Tetramorium blochmanni continentis* Forel. In a dome-shaped termitary of *Cubitermes tenuiceps* (Sjöstedt) (J. Bequaert)—Belgian Congo (Bequaert 1913).
- Tetramorium guineense* (Fabricius). In a dome-shaped termitary of *Cubitermes pallidiceps* (Sjöstedt) (J. Bequaert)—Belgian Congo (Bequaert 1913).
- Tetramorium guineense* var. *indicum* Forel. In abandoned mound termitaries (H. v. Buttel-Reepen)—Sumatra (Forel 1913).
- Tetramorium termitobium* Emery. In a termitary of *Cubitermes sankuruensis* Wasmann (E. Luja)—Belgian Congo (Emery 1893).
- Xiphomyrmex tortuosus* (Roger) var. *ethicus* Forel. With *Odontotermes horni* (Wasmann) under a stone (K. Escherich)—Ceylon (Forel 1911).
- Wasmannia sigmoidea* Mayr. With *Anoplotermes ater* (Hagen) (J. P. Schmalz)—Southern Brazil (Wasmann 1915).
- Cataulacus huberi herteri* Forel. In a dome-shaped, clay termitary partly occupied by *Nasutitermes (Coarctotermes) contractus* (Sjöstedt) (J. Bequaert)—Belgian Congo (Bequaert 1913).
- Cataulacus pygmaeus lujae* Forel. In an abandoned carton termitary on a tree trunk (J. Bequaert)—Belgian Congo (Bequaert 1925).
- Cataulacus taprobanæ* F. Smith. Under bark in a carton termitary of *Nasutitermes ceylonicus* (Holmgren) (K. Escherich, E. Bugnion)—Ceylon (Forel 1911).
- Strumigenys godeffroyi* Mayr. With *Nasutitermes (Hospitalitermes) umbrinus* form *sharpi* Holmgren and in fungus gardens of *Odontotermes javanicus* Holmgren (H. v. Buttel-Reepen)—Malacca and Java (Forel 1913).
- Strumigenys crassicornis* Mayr. With *Anoplotermes ater* (Hagen) (J. P. Schmalz)—Southern Brazil (Wasmann 1915).
- Strumigenys denticulata* Mayr. With *Anoplotermes ater* (Hagen) (J. P. Schmalz)—Southern Brazil (Wasmann 1915).
- Strumigenys lujae* Forel. In a termitary of *Odontotermes monodon lujanus* (Wasmann) (E. Luja)—Mozambique (Wasmann 1902).

- Strumigenys subdentata* Mayr. With *Anoplotermes ater* (Hagen) (J. P. Schmalz)—Southern Brazil (Wasmann 1915).
Epitritus clypeatus Szabó var. *malesianus* Forel. In an earthy carton termitary of *Amitermes dentatus* (Haviland) (H. v. Buttet-Reepen)—Sumatra (Forel 1913).
Proatta butteli Forel. Sifted from an earthy carton termitary of *Amitermes dentatus* (Haviland) (H. v. Buttet-Reepen)—Sumatra (Forel 1913).
Cyphomyrmex rimosus fuscus Emery. With *Anoplotermes ater* (Hagen) (J. P. Schmalz)—Southern Brazil (Wasmann 1915).

Dolichoderinae

- Aneuretus butteli* Forel. A single female specimen from a termitary of *Heterotermes ceylonicus* Holmgren (H. v. Buttet-Reepen)—Ceylon (Forel 1913).
Dolichoderus (Hypoclinea) lutosus (F. Smith) var. *ruficauda* var. nov. In an abandoned arboreal termitary of *Nasutitermes ephratae* (Holmgren) (W. M. Wheeler and I. Molino)—Panama.
Dolichoderus (Monacis) bispinosus (Olivier). In abandoned arboreal termitaries of *Nasutitermes ephratae* (Holmgren) (W. M. Wheeler and I. Molino)—Panama; occupying half a termitary of *N. columbicus* (Holmgren) on palm (A. E. Emerson)—Panama.
Dolichoderus (Monacis) debilis parabioticus Forel. In an inhabited arboreal termitary of *Nasutitermes ephratae* (Holmgren) (W. M. Wheeler and A. E. Emerson)—Panama; in superficial cells of termitaries of *N. corniger* Motschulsky and *N. columbicus* (Holmgren) (A. E. Emerson)—Panama.
Dolichoderus (Monacis) laminatus (Mayr). Frequently in arboreal termitaries of *Nasutitermes ephratae* (Holmgren) (W. M. Wheeler and I. Molino)—Panama.
Leptomyrmex fragilis Emery. Occupying an abandoned termitary and its immediate surroundings (W. Karawaiew)—Aru Archipelago (Karawaiew 1926).
Iridomyrmex chasci Forel. In lower portions of many conical termitaries (W. M. Wheeler)—West Australia.
Iridomyrmex chasci yalgooënsis Forel. In termitaries (L. Glauert)—West Australia.
Iridomyrmex humilis Mayr. Inhabiting wholly or in part many termitaries of *Amitermes hastatus* Haviland (Van der Merwe)—Cape Province (Fuller 1915).
Iridomyrmex sanguineus Forel. Regularly in termitaries of *Drepano-*

- termes silvestrii* Hill and *Amitermes wilsoni* Hill (W. M. Wheeler and G. F. Hill)—Queensland (Wheeler 1918, Hill 1922).
- Bothriomyrmex wroughtoni* Forel. In abandoned fungus-chambers of *Macrotermes gilvus* Hagen (H. v. Buttell-Reepen)—Malacca (Forel 1913).
- Tapinoma heyeri* Forel. With *Nasutitermes fulviceps* (Silvestri) (C. Heyer)—Southern Brazil (Wasmann 1902, 1915).
- Tapinoma indicum* Forel. In fungus gardens of *Odontotermes grandiceps* Holmgren (H. v. Buttell-Reepen)—Java (Forel 1913); in a termitary of *Coptotermes travians* (Haviland) (J. Assmuth)—India (Wasmann 1915).
- Tapinoma luridum longiceps* Wheeler. In an abandoned carton termitary on tree. (Lang, Chapin and Bequaert)—Belgian Congo (Wheeler 1922).
- Tapinoma melanocephalum* (Fabricius) var. *malesianum* Forel. In termitaries (H. v. Buttell-Reepen)—Java (Forel 1913); in termitaries of *Termes* sp.? and *Odontotermes javanicus* Holmgren (N. A. Kemner)—Java.
- Technomyrmex albipes* (F. Smith). In a termitary of *Nasutitermes ceylonicus* (Holmgren) (K. Escherich)—Ceylon (Forel 1911); under bark with *Odontotermes horni* Wasmann (W. Horn)—Ceylon (Wasmann 1902).
- Technomyrmex butteli* Forel. In a damp, woody, carton termitary of *Nasutitermes* (*Hospitalitermes*) *butteli* (Holmgren) (H. v. Buttell-Reepen)—Sumatra (Forel 1913).
- Technomyrmex nigriventris* Santschi. In a conical, clay, inhabited termitary (J. Bequaert)—Belgian Congo (Bequaert 1925).

Formicinae

- Anoplolepis longipes* (Jerdon). In mound termitaries of *Odontotermes* (*Cyclotermes*) *redemanni* Wasmann (W. Horn)—Ceylon (Wasmann 1902); "in almost every termitary" of *O. redemanni* (K. Escherich)—Ceylon (Escherich 1911).
- Plagiolepis exigua* Forel. In galleries of *Nasutitermes matangensis* Haviland and an earthy carton termitary of *Termes propinquus* (Holmgren) (H. v. Buttell-Reepen)—Sumatra (Forel 1913).
- Acantholepis capensis* Mayr. In an abandoned termitary of *Cubitermes sankuruensis* Wasmann (J. Bequaert)—Belgian Congo (Bequaert 1913).
- Acropyga* (*Acropyga*) *acutiventris* Roger var. *flava* Mayr. In a termitary (N. A. Kemner)—Java.

- Acropyga (Atopodon) butteli* Forel. In a woody carton termitary of *Capritermes nemorosus* (Haviland) (H. v. Buttel-Reepen)—Malacca (Forel 1913).
- Acropyga (Atopodon) inezae* Forel. In cavities of an earthy carton termitary of *Termes propinquus* (Holmgren) (H. v. Buttel-Reepen)—Eastern Sumatra (Forel 1913).
- Acropyga (Atopodon) termitobia* Forel. In a cavity of a woody carton termitary of *Capritermes nemorosus* (Haviland) (H. v. Buttel-Reepen)—Malacca (Forel 1913).
- Brachymyrmex admotus* Mayr. With *Nasutitermes fulviceps* (Silvestri) and *Anoplotermes ater* (Hagen) (J. P. Schmalz)—Southern Brazil (Wasmann 1915).
- Brachymyrmex heeri* Forel var. *termitophilus* Forel. With *Anoplotermes ater* (Hagen) and *Nasutitermes fulviceps* (Silvestri) (C. Heyer)—Southern Brazil (Forel 1895, Wasmann 1902, 1915).
- Brachymyrmex incisus* Forel. In peripheral, deserted cells of a termitary of *Nasutitermes corniger* Motschulsky (A. E. Emerson)—Panama.
- Brachymyrmex longicornis* Forel var. *hemiops* Santschi. In a termitary of *Termes panamaënsis* (Snyder) (A. E. Emerson)—Panama.
- Brachymyrmex myops* Emery. With *Nasutitermes fulviceps* (Silvestri) and *Anoplotermes ater* (Hagen) (J. P. Schmalz)—Southern Brazil (Wasmann 1915).
- Brachymyrmex patagonicus* Mayr var. With *Anoplotermes ater* (Hagen) and *Nasutitermes fulviceps* (Silvestri) (J. P. Schmalz, A. Goeldi)—Southern Brazil (Wasmann 1902, 1915).
- Opisthopsis haddoni* Emery. In termitaries (E. Mjöberg)—North-western Australia and Queensland (Forel 1915); nearly always in basal galleries of conical termitaries of *Amitermes wilsoni* Hill (W. M. Wheeler)—Queensland (Wheeler 1918).
- Phasmomyrmex (Myrmorhachis) paradoxus* (Ern. André). In small conical termitaries (Lang and Chapin)—Belgian Congo (Wheeler 1922).
- Camponotus (Tanaemyrmex) barbatus* Roger. In mantle of a clay mound termitary of *Odontotermes (Cyclotermes) obsesus* Rambur (J. Assmuth)—India (Wasmann 1915).
- Camponotus (Tanaemyrmex) congolensis* Emery. In a fungiform termitary of *Cubitermes sankuruensis* Wasmann (J. Bequaert)—Belgian Congo (J. Bequaert 1913).
- Camponotus (Tanaemyrmex) irritans* (F. Smith). In a mound termitary of *Macrotermes gilvus* subsp. *malayanus* (Haviland) (H. v. Buttel-Reepen)—Malacca (Forel 1913).

- Camponotus (Tanaemyrmex) irritans tinctus* (F. Smith) var. *gilvinotus* Forel. Incipient colony in mantle of a termitary of *Macrotermes gilvus* (Hagen) (H. v. Buttel-Reepen)—Sumatra (Forel 1913).
- Camponotus (Tanaemyrmex) irritans tinctus* var. *subnudus* Emery. In termitaries of *Nasutitermes matangensis* Haviland and *N. havilandi* (Desneux) (H. v. Buttel-Reepen)—Sumatra (Forel 1913).
- Camponotus (Tanaemyrmex) maculatus radamoides* Forel var. *liocnemis* Emery. In an abandoned dome-shaped termitary (J. Bequaert)—Belgian Congo (Bequaert 1913).
- Camponotus (Tanaemyrmex) punctulatus termitarius* Emery. Common in termitaries of *Nasutitermes fulviceps* (Silvestri), *Anoplotermes ater* (Hagen), *A. meridianus* Emerson, *A. cingulatus* (Burmeister), *A. tenebrosus* (Hagen) and *Cornitermes similis* (Hagen) (Schupp, Heyer, Dutra, v. Ihering, Silvestri)—Southern Brazil (Wasmann 1902, 1915, Silvestri 1902, 1903).
- Camponotus (Tanaemyrmex) substitutus* Emery. Repeatedly in termitaries of *Nasutitermes* sp. (C. Heyer)—Southern Brazil (Wasmann 1902).
- Camponotus (Tanaemyrmex) variegatus* (F. Smith) var. *mitis* (F. Smith). With *Odontotermes javanicus* Holmgren (N. A. Kemner). Java; in mound termitaries of *Odontotermes (Hypotermes) obscuriceps* (Wasmann) (K. Escherich)—Ceylon (Forel 1911).
- Camponotus (Myrmosericus) rufoglaucus* (Jerdon). In mound termitaries of *Odontotermes (Cyclotermes) redemanni* (Wasmann) (W. Horn)—Ceylon (Wasmann 1902); usually in mantle portions of termitaries (K. Escherich)—Ceylon (Escherich 1911).
- Camponotus (Myrmosericus) rufoglaucus paria* Emery. Usually in mantle portion of termitaries (K. Escherich)—Ceylon (Escherich 1911); in termitary of *Macrotermes gilvus malayanus* Haviland (H. v. Buttel-Reepen)—Malacca (Forel 1913).
- Camponotus (Myrmosericus) rufoglaucus cinctellus* (Gerstäcker) var. *paucipubens* Santschi. In an abandoned dome-shaped termitary (J. Bequaert)—Belgian Congo (Bequaert 1913).
- Camponotus (Myrmosericus) rufoglaucus cinctellus* var. *rufigenis* Forel. In an abandoned dome-shaped termitary (J. Bequaert)—Belgian Congo (Bequaert 1913).
- Camponotus (Myrmothrix) cingulatus* Mayr. In earthen termitaries of *Armitermes heyeri* Wasmann MS (C. Heyer)—Southern Brazil (Wasmann 1902).
- Camponotus (Myrmophyma) claripes* Mayr var. In a termitary (L. Glauert)—West Australia.

- Camponotus (Myrmophyma) discors* Forel. In a termitary (L. Glauert)—West Australia.
- Camponotus (Myrmophyma) ephippium* (F. Smith) var. In a termitary (L. Glauert)—West Australia.
- Camponotus (Myrmophyma) evae* Forel var. In a termitary (L. Glauert)—West Australia.
- Camponotus (Myrmophyma) rubiginosus* Mayr. In dome-shaped termitaries of *Drepanotermes silvestrii* Hill (W. M. Wheeler)—Queensland (Wheeler 1918).
- Camponotus (Myrmophyma) testaceipes* (F. Smith). In a termitary (L. Glauert)—West Australia.
- Camponotus (Orthonotomyrmex) sericeus opaciventris* Mayr. In mantle portions of termitaries of *Odontotermes (Cyclotermes) redemanni* Wasmann (K. Escherich)—Ceylon (Forel 1911, Escherich 1911).
- Camponotus (Myrmopelta) vividus* (F. Smith). In an earthy carton termitary of *Microcerotermes edentatus* Wasmann at top of a tree (E. Luja)—Belgian Congo (Wasman 1911); in large carton termitary on tree (Lang and Chapin)—Belgian Congo (Wheeler 1922).
- Camponotus (Myrmopelta) vividus reginae* Forel. In an abandoned carton termitary of *Microcerotermes bequaertianus* (Sjöstedt) (J. Bequaert)—Belgian Congo (Bequaert 1913).
- Camponotus (Myrmepiromis) fulvopilosus* Emery var. *flavopilosus* Forel. With termites (L. Schultze)—Kalahari Desert, Bechuana-land (Forel 1910).
- Camponotus (Myrmepiromis) nivcosetosus* Mayr, var. From earthen termitaries of *Amitermes unidentatus* (Wasmann) (J. O'Neil)—Cape Province (Wasmann 1902).
- Camponotus (Myrmotrema) grandidieri ruspolti* Forel var. *rollei* Forel. In an abandoned dome-shaped termitary (J. Bequaert)—Belgian Congo (Bequaert 1913).
- Camponotus (Myrmotrema) perrisi jucundus* Santschi. In large conical and fungiform termitaries of *Cubitermes* sp. (Lang and Chapin) (see Fig. 8)—Belgian Congo (Wheeler 1922).
- Camponotus (Myrmotrema) perrisi jucundus* var. *grandior* Forel. In an abandoned dome-shaped termitary (J. Bequaert)—Belgian Congo (Bequaert 1913); in small fungiform termitaries (Lang and Chapin)—Belgian Congo (Wheeler 1922).
- Camponotus (Myrmamblys) agonias* Santschi var. *chapini* Wheeler. In small conical termitaries (Lang and Chapin)—Belgian Congo (Wheeler 1922).
- Camponotus (Myrmamblys) confluens* Forel. In a dome-shaped termitary (J. Bequaert)—Belgian Congo (Bequaert 1913).

- Camponotus (Myrmamblys) confluens* var. *bequaerti* Forel. In a dome-shaped termitary (J. Bequaert)—Belgian Congo (Bequaert 1913).
- Camponotus (Myrmamblys) lilianae* Forel. In an abandoned dome-shaped termitary (J. Bequaert)—Belgian Congo (Bequaert 1913).
- Camponotus (Myrmamblys) reticulatus* Roger var. *latitans* Forel. In a termitary of *Nasutitermes ceylonicus* (Holmgren) (K. Escherich)—Ceylon (Forel 1911).
- Camponotus (Myrmosphinctus) sexguttatus* (Fabricius). With *Nasutitermes fulviceps* (Silvestri) (C. Heyer)—Southern Brazil (Wasmann 1902).
- Camponotus (Myrmaphaenus) novogranadensis* Mayr. In earthen termitaries of *Armitermes heyeri* Wasmann MS (C. Heyer)—Southern Brazil (Wasmann 1902); in a large termitary of *Armitermes excellens* Silvestri on tree trunk, with *Microdon* larvae in galleries (A. E. Emerson and W. M. Wheeler)—British Guiana; common in arboreal termitaries of *Nasutitermes cphratae* (Holmgren) (W. M. Wheeler, A. E. Emerson, I. Molino)—Panama; in termitaries of *Microcerotermes arboris* Emerson (A. E. Emerson and Miss L. Hare)—Panama and British Guiana.
- Camponotus (Myrmaphaenus) personatus* Emery. In termitaries (Schupp)—Southern Brazil (Wasmann 1902, 1915).
- Camponotus (Pseudocolobopsis) macilentus* (F. Smith) var. *castellanus* Wheeler. In galleries in dead branches of *Bursera graveolens* abandoned by *Calotermes pacificus* Banks (W. M. Wheeler)—Galapagos Islands (Wheeler 1924).
- Camponotus (Pseudocolobopsis) macilentus* var. *sapphirinus* Wheeler. In galleries in twigs of *Maytenus obovata* abandoned by *Calotermes pacificus* Banks (W. M. Wheeler)—Galapagos Islands (Wheeler 1924).
- Calomyrmex albertisi* Emery. In dome-shaped termitaries of *Drepanotermes silvestrii* Hill (W. M. Wheeler)—Queensland (Wheeler 1918).
- Calomyrmex splendidus purpureus* Mayr. Several colonies nesting in basal portions of conical termitaries (W. M. Wheeler)—West Australia.
- Polyrhachis (Campomyrma) clypeata* Mayr. In mound termitaries of *Odontotermes (Cyclotermes) redemanni* (Wasmann) (W. Horn)—Ceylon (Wasmann 1902).
- Polyrhachis (Campomyrma)* sp. nov. near *micans* Mayr. In a termitary (L. Glauert)—West Australia.
- Polyrhachis (Chariomyrma) arcuata* Le Guillou. In a mound termitary of *Macrotermes gilvus* (Hagen) (H. v. Buttel-Reepen)—Eastern Sumatra (Forel 1913).

- Polyrhachis (Chariomyrma) aurea* Mayr. In conical termitaries of *Amitermes wilsoni* Hill (W. M. Wheeler)—Queensland.
- Polyrhachis (Chariomyrma) gab* Forel. In conical termitaries of *Amitermes wilsoni* Hill (W. M. Wheeler)—Queensland.
- Polyrhachis (Chariomyrma) gab* var. *senilis* Forel. In conical termitaries of *Amitermes wilsoni* Hill (W. M. Wheeler)—Queensland.
- Polyrhachis (Chariomyrma) gab* var. *tripellis* Forel. In conical termitaries of *Amitermes wilsoni* Hill (W. M. Wheeler)—Queensland.
- Polyrhachis (Chariomyrma) urania* Forel. In conical termitaries of *Amitermes wilsoni* Hill (W. M. Wheeler)—Queensland.
- Polyrhachis (Myrma) militaris* (Fabricius). In a fungiform termitary of *Cubitermes* sp. (Lang and Chapin)—Belgian Congo (Wheeler 1922).
- Polyrhachis (Myrma) orsyllus* F. Smith. In termite galleries (H. v. Buttel-Reepen)—Malacca (Forel 1913).
- Pseudolasius amblyops* Forel var. *sundaicus* Forel. In a termitary of *Capritermes* sp. (N. A. Kemner)—Java.
- Pseudolasius butteli* Forel. In an earthy carton termitary of *Pseudocapritermes angustignathus* (Holmgren) (H. v. Buttel-Reepen)—Malacca (Forel 1913).
- Pseudolasius ludovici* Forel. In a termitary of *Homallotermes foraminifer* (Haviland) (H. v. Buttel-Reepen)—Malacca (Forel 1913).
- Pseudolasius pheidolinus* Emery. In a termitary of *Nasutitermes* sp. (N. A. Kemner)—Java.
- Pseudolasius pygmaeus* Forel. Under a termitary of *Capritermes minor* Holmgren (H. v. Buttel-Reepen)—Sumatra (Forel 1913).
- Nylanderia butteli* Forel. With *Coptotermes travians* (Haviland) (H. v. Buttel-Reepen)—Sumatra (Forel 1913).
- Nylanderia minutula atomus* (Forel). In a termitary of *Termes* sp.? (N. A. Kemner)—Java.
- Nylanderia tapinomoides* (Forel). In a termitary of *Microcerotermes* sp. (N. A. Kemner)—Java.
- Nylanderia vividula* (Nylander), subsp. nov.? In outside cells of termitary of *Amitermes medius* Banks. (A. E. Emerson)—Panama.

APPENDIX C

A NOTE ON "IMITATION" AMONG THE SOCIAL INSECTS

Authors still occasionally attempt to account for the unusual similarities of structure and behavior among animals of widely diverse phylogenetic origins as the result of "imitation." Biologists, however, except in the cases of protective resemblance and mimicry, which are supposed to be caused by natural selection, explain such similarities, variously designated as 'parallel,' 'convergent,' 'analogical,' 'homoplastic' or 'typovergent,' as independent adaptations to very similar environmental conditions. This view is supported by the great difficulties encountered by psychologists and behaviorists in detecting any unequivocal evidence, except in the higher vertebrates, of actual copying or imitation of the behavior of individual animals by their fellows. It is, of course, even more difficult to furnish proof of the imitation of one animal species as a whole or of one social organization by another. The extraordinary resemblances between the societies of ants, one of the most specialized families of the highest order of insects, and of termites, the most specialized among the lowest insects, are therefore liable to lead only the unwary to assume some mutual or unilateral imitation as the cause of their similarities. Though I am willing to accept responsibility for a certain amount of confusion on the part of my readers, because in several of my writings I have stressed the remarkable parallelisms between ant and termite societies, I cannot plead guilty to having failed at the same time to emphasize their structural and behavioristic differences. In two places in the second part of this paper I have added to the list of resemblances by calling attention to certain analogies between the *Carebara* and termite queens (p. 202) and to the singular termitoid physogastry of the queen and workers of *Stigmatopora termitoxenus* (p. 215). One of the authors who may have misinterpreted some of my expressions and perhaps also those of writers like Willey (1911, p. 119), who has maintained that "no example of bionomical convergence is more remarkable than that which is presented by the social insects, the ants, bees, wasps and termites," is Prof. G. N. Lewis. In a passage near the end of his illuminating Silliman Lectures (1926) he offers the following comments:

"Let us now turn our attention to another phenomenon which I have chosen, not merely because it is curious, but because its discovery is one of those crucial observations which has the power to change our whole attitude towards nature. Various authors have mentioned the numerous cases of apparent imitation of one species by

another, but there is one case which is far more significant than all of the others that have been observed. If I should ask you what animal it is that has learned self-sacrifice and loyalty, that has developed a great industrial system with special laboring and military classes, that has built great structures fifty or a hundred times his own height, that has domesticated animals, and created an agriculture, with species of plants not to be found in the wild state, you would probably say it is man; but man has been doing some of these things only a very few thousand years, while these same arts have been practiced for a million years by a lowly insect whose nearest relatives are the book louse and the cockroach. I refer to the termites, which are sometimes called white ants because of their remarkable resemblance in habits to the ant family. Yet the termites and the ants come at the very opposite ends of the classification of insects.

"The resemblance is so extraordinary that Professor Wheeler writes, 'it is as if we had found, when Australia was first explored, the kangaroos and opossums enjoying a social organization like that of man.'" To ignore such a remarkable phenomenon is unscientific, to call it a coincidence is anti-scientific. To apply repeatedly and against all principles of chance the hypothesis of coincidence is the very negation of science. If we had observed merely that the termites have a social organization, and that the group of insects to which ants, bees and wasps belong also have a social organization, it would be interesting. If it were observed that the termites and the ants are the only insects which cut off their wings after mating, this might be a coincidence. But when we find that termites and ants have a cultural life which is almost identical; that each has its royal, worker and soldier castes; that they have similar complicated methods of deriving sustenance from one another; similar building habits, with elaborate ventilated gardens in which are grown and cultivated fungi unknown in the wild state, and similar domesticated insects, how can we harbor even the suggestion of coincidence?

"The parallel cited by Professor Wheeler is not quite exact. Supposing that, when Australia was discovered, we had found men and kangaroos building mud structures of the same architectural type, burying their dead in similar mounds and with like ceremonials, would we doubt that one of these species had exerted a profound cultural influence upon the other? Now ants and termites often live together in a happy symbiosis, and, indeed, there are certain species of ants which have been found only in the termitaria. These facts give us a feeling akin to that experienced by Robinson Crusoe when

he found the footprints on his desert island. I do not claim that imitation is the only possible explanation of this curious phenomenon, but I shall be surprised if any other can be presented which will do less violence to our established ways of thought."

It would be ungracious to criticize a few inaccuracies and exaggerations in these paragraphs, since their author is not an entomologist but a distinguished physicist and chemist, or to dwell on the vagueness of his imitation hypothesis. Prof. Lewis does not tell us whether he conceives the ants to have been imitating the termites or the termites the ants, or whether the imitation has been mutual during the long, parallel evolution of the two groups since Cretaceous times. We find difficulty, too, in understanding how imitation could account for some of the most striking convergences, such as fungus culture, which is practiced only by a single tribe of ants confined to America and only by certain genera of termites confined to tropical Africa and Indomalaya, unless we assume that one of these groups of fungus-growers ranged over both hemispheres during some past geological age. Of course, this is not altogether improbable, but since ants so very, very rarely, and not "often" as Prof. Lewis avers, live in "a happy symbiosis with termites," it is difficult to imagine how there can be any imitation either mutual or unilateral, or how the sterile workers, which in both ants and termites control the growth and social organization of their respective colonies, could transmit what they have learned by imitation to subsequent generations. Even more formidable difficulties appear in the convergent association of ants and termites with certain guests (myrmecophiles and termitophiles), which among themselves exhibit most extraordinary typovergent developments, such as trichomes, exudatoria and symphilic coloration, not only in species of very diverse phyletic affinities but also among those definitely associated with different host ants and termites and therefore precluded from imitating other species of guests.

The conventional biological explanation of such phenomena is far simpler as I have indicated in the cases of *Carebara* and *Stigmatococcus*, which on Prof. Lewis' hypothesis would have to be regarded as imitators of their termite hosts. The species of *Carebara* live only in termitaries and have huge females because the diminutive, blind workers are able to secure an unusually abundant supply of rich food and not because they are aware of the enormous termite queens and set about rearing females of comparable dimensions in their own nests. Nor can we believe that the queen and workers of *Stigmatococcus* are

induced to become physogastric by imitating their termite hosts, since this phenomenon is far more probably the direct result of regurgitative overfeeding by the host workers. Of course, there may be adjuvant causes of the physogastry, such as the presence of growth hormones in the food administered to the female *Carebara* larvae or to the adult queen and workers of *Stigmatopora*. Certainly such an explanation will be far more acceptable to the biochemist and physiologist, and even to the behaviorist, than Prof. Lewis' imitation hypothesis. It would not be difficult to show that the nesting habits, the caste system and its physiological division of labor, the toleration of the guests, the nuptial and dispersion flights, the methods of colony founding and other typovergent peculiarities of ants, termites, social bees and wasps can all be accounted for in a like manner as independent adaptations to recurring, similar conditions if we make due allowance for the common basic similarities of structure and function among solitary insects and for the similarities of organization and behavior which necessarily follow the adoption of a communal or social mode of life by the individuals thus constituted.

LITERATURE CITED

- ARNOLD G. 1914. Nest-changing Migrations of Two Species of Ants. *Proc. Rhodesia Sc. Assoc.* 13, pp. 25-42, 3 figs.
- ARNOLD, G. 1915-1926. A Monograph of the Formicidae of South Africa. *Ann. S. Afric. Mus.* 14.
- BEQUAERT, J. 1913. Notes biologiques sur quelques fourmis et termites du Congo Belge. *Rev. Zool. Afric.* 2, pp. 396-431, 6 figs.
- BEQUAERT, J. 1925. Notes detachées sur la biologie des fourmis congolaises. *Rev. Zool. Afric.* 13, pp. 133-149.
- BEQUAERT, J. 1926. Medical and Economic Entomology, in *Medical Report of the Hamilton Rice Seventh Expedition to the Amazon*. Harvard Univ. Press, p. 183.
- BINGHAM, C. T. 1903. The Fauna of British India, including Ceylon and Burma. Hymenoptera Vol. II. London, Taylor and Francis.
- BÜNZLI, G. H. 1935. Untersuchungen über coccophile Ameisen aus den Kaffeefeldern von Surinam. *Mitteil. Schweiz. Ent. Gesell.* 76, pp. 455-593, 51 figs.
- BUGNION, E. 1922. La guerre des fourmis et des termites. La genèse des instincts expliquée par cette guerre. Appendix to Forel's "Monde sociale de fourmis" Tome 3, pp. 173-225; In Ogden's translation vol. 2, pp. 353-404.
- CLARK, J. 1925. The Ants of Victoria. Part I. *Victorian Naturalist* 42, p. 58-64.
- COLLART, A. 1925. Quelques observations sur les fourmis *Megaponera*. *Bull. Cercle Zool. Congolais* 2, pp. 26-28.

- COLLART, A. 1927. Notes sur la biologie des fourmis congolaises. *Rev. Zool. Afric.* 14, pp. 249-253.
- EMERSON, A. E. 1925. The Termites of Kartabo, Bartica District, British Guiana. *Zoologica* 6, no. 4, pp. 291-459, 94 figs. 1 pl.
- EMERSON, A. E. 1928. Termites of the Belgian Congo and the Cameroon. *Bull. Amer. Mus. Nat. Hist.* 57, pp. 401-574, 78 figs., 24 maps, 19 pls.
- EMERY, C. 1890. Voyage de M. E. Simon au Venezuela. (Decembre 1887-Avril 1888). Formicides. *Am. Soc. Ent. France*, p. 71.
- EMERY, C. 1893. Zusammensetzung und Entstehung der Termitengesellschaften. *Biol. Zentralbl.* 13, pp. 758-766.
- EMERY, C. 1901. Ameisen gesammelt von Dr. W. Horn 1889. *Deutsch. Ent. Zeitschr.* pp. 113-122, 4 figs.
- EMERY, C. 1911. Ponerinae, in Wytsman's "Genera Insectorum." Fasc. 118.
- ESCHERICH, K. 1911. Termitenleben auf Ceylon. Jena, Gustav Fischer.
- ESCHERICH, K. 1917. Die Ameise. Schilderung ihrer Lebensweise, 2. Aufl. Braunschweig 1917.
- FOREL, A. 1869. Observations sur les moeurs du *Solenopsis fugax*. *Bull. Soc. Suisse Ent.* 3, p. 105.
- FOREL, A. 1874. Les fourmis de la Suisse. *Nouv. Mém. Soc. Helvetique Sc. Nat.* 26. Zürich 452 pp. 2 pls.
- FOREL, A. 1894. Einige neue Ameisen aus Südbrasilien, Java, Natal und Mossamedes. *Mitth. schweiz. Ent. Gesell.* 10, pp. 297-311.
- FOREL, A. 1895. Beschreibung einiger neuen brasilianischen Ameisenarten, in Wasmann's "Die Ameisen-und Termitengäste von Brasilien." *Verhandl. zool. bot. Ges. Wien* 45, pp. 178-179.
- FOREL, A. 1895a. Nouvelles fourmis d'Australie recoltées à The Ridge, Mackay, Queensland par M. Gilbert Turner. *Ann. Soc. Ent. Belg.* 39, pp. 417-428.
- FOREL, A. 1901. Fourmis termitophages, lestiobiase, *Atta tardigrada*, sous-genre d'Euponera. *Ann. Soc. Ent. Belg.* 45, pp. 389-398, 1 fig.
- FOREL, A. 1902. Variétés Myrmécologiques. *Ann. Soc. Ent. Belg.* 46, pp. 284-296.
- FOREL, A. 1910. Formicidae, in L. Schultze, "Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Südafrika (1903-1905)," 4, pp. 3-30, 7 pl.
- FOREL, A. 1911. Sur le genre *Metapone* n. g. *Rev. Suisse Zool.* 19, pp. 445-459, 1 pl.
- FOREL, A. 1911a. Ameisen aus Ceylon. In K. Escherich's "Termitenleben auf Ceylon," Jena, K. Fischer, pp. 215-228.
- FOREL, A. 1915. Ameisen, In "Results of Dr. E. Mjöberg's "Swedish Scientific Expeditions to Australia 1910-1913." *Ark. f. Zool.* 9, pp. 1-119, 6 figs, 1 pl.
- FOREL, A. 1921-1922. Le monde sociale des fourmis du globe. 5 vols. Genève, Kundig. Trans. by C. K. Ogden, 2 vols. London and New York, Putnam's.

- FULLER, C. 1915. Observations on some South African Termites. Ann. Natal Mus. 3, pp. 329-504, 11 pls., 16 figs.
- GALLARDO, A. 1918. Las hormigas de la Republica Argentina. Sub-familia Ponerinas. Anal. Mus. Nat. Buenos Aires 30, pp. 1-67, figs. 14 and 15.
- Ghesquière, J. 1922. (On *Megaponera foetens* and *Atopomyrmex*.) In Hegh, "Les Termites" (q. v.) pp. 578-579.
- HAYES, W. P. 1920. *Solenopsis molesta* Say, a Biological Study. Techn. Bull. No. 7, Agric. Exper. Station Kansas State Agric. Coll. 55 pp., 11 figs.
- Hegh, E. 1922. Les Termites. Partie Générale. Brussels.
- HILL, G. F. 1922. Australian Termites of the Genera Drepanotermes, Hamitermes and Leucotermes. Bull. Ent. Research 12, pp. 363-399, 31 figs., 3 pls.
- HOLMGREN, N. 1912. Termitenstudien. 3. Systematik der Termiten. Die Familie Metatermitidae. K. Svensk. Vetensk. Handl. 48, pp. 1-166, 4 pls., 88 figs., 18 diagrams.
- JANET, C. 1897. Rapports des animaux myrmécophiles avec les fourmis. Limoges, 99 pp.
- KARAWAIEW, W. 1926. Ameisen aus dem Indo-Australischen Gebiet. Treubia 8, pp. 430-433, 7 pl. 12 figs.
- KING, G. B. 1895. The Study of the Formicidae of Lawrence, Mass. Ent. News 6, pp. 220-223.
- LEWIS, G. N. 1926. The Anatomy of Science. New Haven, Yale University Press.
- LIVINGSTONE, D. 1859. Missionary Travels and Researches in South Africa.
- MAIDL, F. 1933. Die Lebensgewohnheiten und Instinkte der staatenbildenden Insekten. Vienna, Fritz Wagner.
- MANN, W. M. 1911. Notes on the Guests of Some California Ants. Psyche 18, pp. 27-31, 1 fig.
- MAYR, G. 1886. Notizen über die Formiciden-Sammlung des British Museum in London. Verhandl. K. K. zool. bot. Ges. Wien, p. 358.
- PRELL, H. 1911. Biologische Beobachtungen an Termiten und Ameisen (von der akademischen Studienfahrt nach Ostafrika, 1910). Zool. Anzeig. 38, pp. 243-253, 4 figs.
- POULTON, E. B. 1916. Dr. G. D. H. Carpenter's Notes on South-West Uganda and on Late German East Africa West of the Victoria Nyanza. Trans. Ent. Soc. London 1916, Proc. p. cxxix.
- RAU, P. 1933. The Jungle Bees and Wasps of Barro Colorado Island (with Notes on Other Insects). St. Louis, Mo.
- ROGER, J. 1861. Die Ponera-artigen Ameisen. Berlin. Ent. Zeitschr. 4, pp. 278-312; 5, pp. 1-54.
- ROTHNEY, A. J. 1889. Notes on Indian Ants. Trans. Ent. Soc. London, pp. 347-374.
- ROTHNEY, A. J. 1895. Notes on Indian Ants. Trans. Ent. Soc. London, pp. 195-217.

- SANTSCHI, F. 1914. Formicidae. In "Voyage de Ch. Alluaud et R. Jeannel en Afrique Orientale. Insectes Hyménoptères II." Paris, A. Schulz. pp. 43-148, 2 pls., 30 figs.
- SANTSCHI, F. 1927. Deux notices sur les fourmis. Bull. Ann. Soc. Ent. Belg. 66, pp. 327-330.
- SCHOUTEDEN, H. 1924. Une fourmi qui razzie les termites (*Megaponera foetens*). Rev. Zool. Afric. 12, Suppl.
- SILVESTRI, F. 1902. Note preliminari sui termitidi e termitofili sudamericani. Boll. Mus. Torino 17, no. 419, p. 24.
- SILVESTRI, F. 1903. Contribuzione alla conoscenza dei termitidi e termitofili dell' America Meridionale. Portici. Redia 7, pp. 1-234.
- SILVESTRI, F. 1923. Descriptiones Termitum in Anglorum Guiana Reperitorum. Zoologica 3, pp. 307-321, 5 figs.
- SJÖSTEDT, Y. 1908. Wissenschaftliche Ergebnisse der schwedischen zoologischen Expedition nach dem Kilimandjaro, dem Meru und den umgebenden Massaiesteppen Deutsch Ostafrikas. 1905-1906.
- SMITH, F. 1858. Catalogue of Hymenopterous Insects in the Collection of the British Museum. Pt. VI Formicidae. London, p. 98.
- VERHOEFF, K. 1925. Wanderungen durch die Wunder der Lebensgemeinschaft. Leipzig, Akadem. Verlagsgesell.
- WASMANN, E. 1901-02. Neues über die zusammengesetzten Nester und gemischten Kolonien der Ameisen. Allgem. Zeitschr. Ent. 6, pp. 353-355, 369-371; 7, 1-5, 33-37, 72-77, 100-108, 136-139, 167-173, 206-208, 235-240, 260-265, 293-298, 340-345, 385-390, 422-427, 441-449, 1 pl.
- WASMANN, E. 1902a. Termiten, Termitophilen und Myrmecophilen gesammelt auf Ceylon von Dr. W. Horn 1899, etc. Zool. Jahrb. Abth. f. Syst. 17, pp. 99-164, 2 pls.
- WASMANN, E. 1911. Zur Kenntnis der Termiten und Termitengäste vom Belgischen Congo. Rev. Zool. Afric. 1, pp. 91-117, 145-176.
- WASMANN, E. 1915. Das Gesellschaftsleben der Ameisen 1. Bd. Münster i. W., Aschendorffsche Verlagsbuchhandlung.
- WELLMAN, F. C. 1908. Notes on Some Angolan Insects of Economic or Pathologic Importance. Ent. News 19, pp. 26-33, 224-230 (*Megaponera foetens* erroneously cited as a *Polyrhachis*).
- WHEELER, W. M. 1900. The Habits of *Ponera* and *Stigmatoma*. Biol. Bull. 2, pp. 43-69, 8 figs.
- WHEELER, W. M. 1901. The Compound and Mixed Nests of American Ants. Amer. Naturalist 35, pp. 431-448, 513-539, 701-724, 791-818, 20 figs.
- WHEELER, W. M. 1903. *Erebomyrma*, a New Genus of Hypogaecic Ants from Texas. Biol. Bull. 4, pp. 137-148, 5 figs.
- WHEELER, W. M. 1904. A Crustacean-eating Ant. (*Leptogenys elongata*) Biol. Bull. 6, pp. 251-257, 1 fig.
- WHEELER, W. M. 1910. Ants, their Structure, Development and Behavior. New York, Columbia Univ. Press.

- WHEELER, W. M. 1914. Note on the Habits of *Liomyrmex*. *Psyche* 21, pp. 75, 76.
- WHEELER, W. M. 1916. Ants collected in British Guiana by the Expedition of the American Museum of Natural History during 1911. *Bull. Amer. Mus. Nat. Hist.* 35, pp. 1-14.
- WHEELER, W. M. 1918. The Australian Ants of the Ponerine Tribe *Cerapachyini*. *Proc. Amer. Acad. Arts Sci.*, 53, pp. 215-265, 17 figs.
- WHEELER, W. M. 1918a. The Ants of the Genus *Opisthopsis* Emery. *Bull. Mus. Comp. Zool.* 62, pp. 341-362, 3 pls.
- WHEELER, W. M. 1922. Ants of the American Museum Congo Expedition. A Contribution to the Myrmecology of Africa. *Bull. Amer. Mus. Nat. Hist.* 45, p. 1-269, 23 pls., 76 figs.
- WHEELER, W. M. 1922a. The Ants of Trinidad. *Amer. Mus. Novitates*, No. 45, pp. 1-16.
- WHEELER, W. M. 1922b. Neotropical Ants of the Genera *Carebara*, *Tranopelta* and *Tranopeltoides*, New Genus. *Amer. Mus. Novitates*, No. 48, pp. 1-14, 3 figs.
- WHEELER, W. M. 1923. Formicidae. In "Wissenschaftliche Ergebnisse der schwedischen Reise des Herrn Dr. A. Roman in Amazonas 1914-1915." *Ark. f. Zool.* 15, pp. 1-6.
- WHEELER, W. M. 1924. The Formicidae of the Harrison Williams Galapagos Expedition. *Zoologica* 4, pp. 111-122, 27 figs.
- WHEELER, W. M. 1933. Colony-founding among Ants, with an Account of some Primitive Australian Species. Harvard University Press.
- WHEELER, W. M. AND MANN, W. M. 1914. The Ants of Haiti. *Bull. Amer. Mus. Nat. Hist.* 33, pp. 1-61, 27 figs.
- WILLEY, A. 1911. *Convergence in Evolution*. New York, E. P. Dutton & Co.
- WROUGHTON, R. C. 1892. Our Ants. *Journ. Bombay Nat. Hist. Soc.* pp. 13-60, 2 pls.

